Life history and reproductive ecology of selected Proteaceae in the mountain fynbos vegetation of the south-western Cape

David Carlyle Le Maitre

A thesis presented in partial fulfilment of the degree of Doctor of Philosophy

in the Faculty of Science, University of Cape Town

Department of Botany

1998

There are no applied sciences...there are only applications of science and this is a very different matter....The application of science is very easy to anyone who is the master of the theory of it

Louis Pasteur 1871 *Revise Scientifique*

« Φ »

I believe that it would be worth trying to learn something about the world even if in trying to do so we should merely learn that we do not know much. This state of learned ignorance might be a help in many of our troubles. It might be well for all of us to remember that, while differing widely in the various little bits that we do know, in our infinite ignorance we are all equal.

Karl Popper 1965 *Conjectures and refutations*

TABLE OF CONTENTS

ABSTRACT

The studies in this thesis recognise the key role of fire as a factor which has shaped the life-histories of plants in fire-prone mediterranean shrublands. Fire regimes are not simply products of the abiotic elements of climate and ignition sources. The biotic component makes a significant contribution because community structure and processes like litter fall determine fuel loads, and fuel distribution, and will determine properties such as fire recurrence intervals and shapes and patchiness of fires.

Another key factor in the evolution of the traits of fynbos plants is plant-animal interactions involving seed and seedling predators or pathogens and herbivory. Because fires have a significant random component (for example in the timing of ignition, the position of the ignition point in the landscape and in relation to the wind movements and post- and pre-fire rainfall patterns), each fire is a unique event. These random factors are overlaid on the probability distributions of the other, more predictable factors. For example both fire recurrence intervals and the seasonal fire frequencies follow predictable pattens and therefore provide a basis for natural selection.

Life-history theory links the evolutionary perspective - why organisms have evolved to be the way they are - and the ecological perspective - how traits function in the current environment. The primary selective pressures in the fynbos environment are nutrient-poor soils, winter rainfall and summer drought, recurrent fires and biotic interactions.

The study can be divided into four sections:
(1) patterns in reproductive maturation and mortality,
(2) seed bank dynamics and pre-dispersal predation by insects,
(3) seed germination and seedling mortality, and
(4) an analysis of the relationship between plant life-histories and fire frequency distributions.

In the first study, mortality rates of *Protea neriifolia*, *P. lacticolor* and *Leucadendron xanthoconus* varied from 13 to 40% from the age of 1-10 years. Mortality rates from 20-30 years of age were similar in all species and significantly higher than for younger plants, providing some support for the idea that these species undergo senescence. The removal of up to 90% of the inflorescences of *Protea lacticolor* and *P. neriifolia* by baboons or rodents reduced seed banks of the proteas but not *Leucadendron xanthoconus*. Seed banks at the age of 10 years, in terms of seeds per shrub were adequate for population replacement except for *P. lacticolor*.

The studies in the second part found that the dynamics of the seed banks of *Protea neriifolia* and *P. repens* differ markedly. The number of full seeds (with a firm white embryo) declines with age in both species. *Protea repens* had many full seeds per inflorescence in the youngest age class, but few full seeds in older inflorescences because of seed predation by insects. *Protea neriifolia* had few full seeds per inflorescence but there was a slow rate of decline in the number of seeds per inflorescence. Although the number of *seeds per shrub* of both species declined with increasing stand density, the number of seeds per square metre increased, more than compensating for the decline in unit output. Inflorescences of *P. repens* experience higher levels of seed predation by insects than those of *P. neriifolia*. Insect infestation levels increased rapidly with increasing age in *P. neriifolia* but were lower in mature plants than in the co-occurring *P. repens*. Low and unpredictable seed set may limit the effects of seed-eating insects on the seed yield of *P. neriifolia* when compared with co-occurring *P. repens*.

The third section examined the germination of planted seeds in a 28-year old shrubland. Germination and establishment before a fire in March 1987 was similar to that after the fire but seedling mortality was higher before the fire. Seedling mortality during the first summer after the fire (October to March) was significantly correlated with planting date, in contrast to the findings of a similar study in the southern Cape. Simulations using a simple empirical model based on indexes of the daily soil moisture balance and temperature showed that a reduction of 10 or 20% in daily rainfall will have little impact on the germination of seeds released in late-summer or autumn in the western Cape, because of the long wet winter period. An increase in daily temperatures could have a more significant impact as it may reduce the length of the favourable period for germination.

The final study compared the life-history traits in seeders and a sprouter. Many studies have identified distinct patterns in the demography and resource allocation patterns of seed-regenerating and sprouting plants which are analogous to the patterns predicted for semelparous and iteroparous species by life-history theory. But there are several ways in which the demography of plants in fire-prone environments violates the assumptions of classical life-history theory. A new approach has been developed which explicitly accommodates these deviations and provides models which predict direct relationships between the probability distribution of fires (in time) and the reproductive maturation, mortality rates and lifespans of seeders and sprouters. A test of these models using data on fire frequencies and the demography of a seed regenerating and a sprouting species of *Protea* shows that they appear to apply to fynbos as well. This opens the door to the development of quantitative models that can provide a consistent theoretical framework for predicting and interpreting the relationships between fire regimes and life-history traits. It also supports arguments

that regeneration exclusively from seeds and by sprouting (and from seeds), and the related suites of traits, are expressions of distinct and divergent life history strategies.

Why is it important to understand life-history strategies? Life-history theory is about how organisms maximise their evolutionary fitness and thus is about organisms allocate their limited resources to survival and reproduction to maximise reproductive success. The theory also provides a link between understanding what an organism is doing and when - as is typically documented in demographic studies - and why it is doing that - which gives a deeper level of insight. There have been numerous studies and reviews of life-history theory which have covered a wide variety organisms, but somehow most of these studies have been based, explicitly or implicitly, on the highly simplified r-K selection models. The studies in Chapter 6 were based on an alternative model which offers new insights into the life-histories of plants in fire prone environments. The current approach to managing fynbos (e.g. how often to burn) is based on observations of plant maturation and recruitment success which are used to determine the desired intervals between fires. Studies of fire-frequencies also have shown that fire intervals follow a definite distribution in time. The intervals determined by these two different approaches are about the same but there has been no direct link. The new life-history based approach makes that link explicit and direct and gives us insights into why there should be a link and what the implications are. For example, what is the likely reproductive success over a range of fire frequencies. The approach still needs further development but it definitely merits further studies.

PREFACE

In this preface I describe my contribution to each of the chapters in this thesis to minimise misunderstandings. I am senior or sole author of all the papers except chapter 1 which was written jointly with CA Jones as an equal contributor. The studies contained in this thesis cover a logical sequence in the reproductive cycle of seed regenerating protea shrubs, beginning with the general demography (chapter 2), seed bank dynamics (chapters 2-4) and the fate of seeds during germination and during and after establishment (chapter 5). Chapter 6 examines life-history based models of the relationship between fire frequency distributions and the reproductive maturation, mortality and lifespans of seeding and a sprouting species in the Proteaceae. Chapter 7 discusses the findings, synthesises them and offers some suggestions for further work.

The scope and nature of some of these studies and papers has necessitated some collaboration with other researchers (the details for each chapter are given below). I detail my contributions to each of these papers here for the information of the thesis examiners.

Chapter 1: Introduction. Exclusively the work of DC Le Maitre (DLM).

Chapter 2: Demography, reproductive development and seed bank dynamics of *Leucadendron xanthoconus*, *Protea neriifolia* and *Protea lacticolor* (Proteaceae) at Jakkalsrivier, south-western Cape. Chapter written by DLM as senior author and CA Jones (CAJ) as co-author. Original experiment planned and laid out by Dr FJ Kruger. Data from 1980-1985 analysed and presented by Dr Kruger in his PhD Thesis. Data collection from 1988, approach, research questions and analyses in this paper largely the work of DC Le Maitre. CAJ was responsible for collating comparative data from other studies (excluding data collated by DLM for chapter 3) and the paper was written jointly.

Chapter 3: Influence of age, size and stand density on canopy-stored seed banks of two co-occurring fynbos shrubs (*Protea repens* and *Protea neriifolia*, Proteaceae) in South Africa. Exclusively the work of DLM.

Chapter 4: A preliminary study of seed production of *Protea neriifolia* (Proteaceae) in Jonkershoek, Stellenbosch, Cape Province, with emphasis on the effects of seed-eating insects. Exclusively the work of DLM.

Chapter 5: Climatic change and seedling recruitment of serotinous Proteaceae: a study of seed

germination and seedling survival in *Protea neriifolia*. Exclusively the work of DLM with extensive support from technical staff and from SA Botha during data collection.

Chapter 6: The possibility of this study was suggested by WJ Bond and the data on the fire frequencies and the reproductive maturation and mortality of the Proteaceae was taken from field data collected by a variety of people. Analyses and writing of the paper exclusively the work of DLM with support from H Diedericks and Dr R Guo who helped resolve some of the difficulties I had in interpreting and applying the life-history models developed by Dr JS Clark.

Chapter 7: Discussion and conclusions. Exclusively the work of DC Le Maitre (DLM).

ACKNOWLEDGEMENTS

This study was supported by the Conservation Research Programme of the Forestry Branch of the Department of Environment Affairs (DEA). During the period of this study the South African Forestry Research Institute (SAFRI) was transferred from the DEA to the Council for Scientific and Industrial Research (CSIR) to form the Division of Forest Science and Technology (Forestek). I would particularly like to thank the Director General (DEA), Dr FJ Kruger the Director Research (SAFRI) and of Forestek, and Mr J Bosch and Dr P Manders for supporting me in the completion of this thesis and for permission to undertake this work and submit it as a thesis.

I thank my supervisors Drs Richard Cowling and William Bond for their enthusiastic support, patience and valuable guidance and criticism and for developing many of my ideas over the years we have known each other. I also want to thank my colleagues at Jonkershoek, particularly Brian van Wilgen, Pat Manders and Dave Richardson for discussions and the effort they put into the editing of various chapters of this thesis. I also want to thank Jeremy Midgley for his thought provoking ideas and advice during the course of these studies. I thank Fanie Botha who was involved in collaborative studies in Swartboskloof. I thank Alan Lamb, Greg Forsyth, Kevin Higgins, Gregory Bailey, Adrian Simmers, Gordon Hockey and Clare Jones for directing and assisting with field work and for reliably carrying out laborious tasks like putting data on the computer and checking it. Clare Jones also gets special thanks for her assistance with checking for errors in the printed copy and for fitting figures into frames. I also thank Anne Green who cheerfully drew and redrew the figures used in this thesis and the published papers.

Last, but certainly not least, I would like to thank my family for their support during the long working hours that accompany the gestation and birth of a thesis. I would particularly like to thank them for bearing with me on the many occasions when I was more distracted, tense and irritable than usual.

Chapter 1: Introduction

During the last 20 years there have been significant advances in our understanding of the demography of the Proteaceae in the fire-prone shrublands of Cape fynbos and Australian kwongan. This is particularly true of the fire ecology and population dynamics of the numerous tall, fire-killed shrub species which retain seeds in their persistent woody fruits (infructescences). The studies in this thesis try to take this understanding a step further by examining particular aspects of the reproductive ecology of *Protea* and *Leucadendron* species. Although we know a great deal more about **how** various species respond to fires, progress in understanding **why** has been slower. I examine seed banks, seedling recruitment and mortality patterns in established plants and then examine how the patterns match the predictions of life-history models developed for fire-prone environments. The following sections briefly review current understanding of disturbance processes and life-history theory and how they relate to the demography of plants in fire-prone ecosystems.

1.1 Ecology and disturbance

A dominant paradigm in ecology has been the concept of the "balance of nature"; that ecosystems are in, or are developing towards, an equilibrium state or climax (e.g. Clements 1916). The prevalence of disturbance was acknowledged but the emphasis was on the processes between disturbances, particularly succession. Researchers of the equilibrium school have developed a substantial body of theory and studies of the driving processes, particularly competition and herbivory, and their effects on communities and species' life-histories (see for example Diamond & Case 1986; Begon *et al.* 1986). In the last 20 years more information has been accumulated on disturbance regimes (frequency, season, intensity) and how they determine ecosystem structure and dynamics (see the review by Pickett & White 1985). This, in turn, has resulted in a greater emphasis on non-equilibrium dynamics and the impacts of stochastic processes, such as lottery recruitment (Chesson & Warner 1981), on ecosystem structure and species traits (Diamond & Case 1986). Fire-prone ecosystems with seed regenerating shrubs provide an ideal environment for studies of fire regimes and the dynamics of seedling recruitment, including fire frequency, fire season and competition and lotteries as explanations for coexistence (see Bond & Van Wilgen 1995 for a recent synthesis).

The observed patterns are an expression of the underlying driving factors that the plants have responded to. Their responses, in turn, have been determined not just the by factors themselves, but by the particular combinations of factors and their distributions in space and time (Gill 1975; Stearns 1977).

1.2 The selective regime in fynbos

The primary selective forces in fynbos, and in the similar kwongan vegetation of Australia, are recurrent fires, low nutrient levels in the soils and summer droughts (Le Maitre & Midgley 1992)

Scarce nutrients

The low levels of nutrients in fynbos soils constrain both plant growth and plant life-cycles, short life cycles such as those of annuals are simply uneconomic (Fitter 1986; Stock and Allsop 1992). Low nutrient levels also limit litter decomposition, resulting in the accumulation of fine woody fuels (Gill 1975) which comprise the main fuel in fynbos (Van Wilgen 1984). Seeds are often an expensive investment (Kuo *et al.* 1982; Stock and Allsop 1992; Witkowski & Lamont 1996) and many plants produce very few but relatively large seeds (Le Maitre & Midgley 1992, Le Maitre 1992; Stock and Allsop 1992).

Winter rainfall and summer drought

Winter rains are brought by extensive cold fronts and are spatially and temporally predictable, promoting the evolution of appropriate cues for seed germination and growth (Westoby 1980). The seasonal predictability of the rainfall and the hot, dry summers also results in temporally predictable fire regimes (Van Wilgen & Burgan 1984).

Fire regime

Recurrent fires are a significant selective force; they result both in mortality and in an increase in the availability of resources for recruitment (Gill 1975). The key components of fire regimes are the frequency, seasonality and intensity of fires (Gill 1975) with fires in fynbos occuring at intervals of 8-20 years (rarely 40+). The important issue for fire frequency and seasonality is that they are predictable (Van Wilgen 1984; Johnson and Van Wagner 1985), providing a basis for selection of plant traits favouring maximum recruitment after fires at the most likely interval and season (Clark 1991). They are also generally shorter than the generation times of species or their propagules (see Southwood 1988). Fire intensity depends primarily on climatic factors and is relatively unpredictable (e.g. Cheney 1981; Van Wilgen *et al.* 1985). The effects of fires on plants are also determined by the influence of post-fire climatic conditions on recruitment (Specht 1981; Christensen 1985). The spatial scale of fire patchiness is coarse from the plants perspective (see Southwood 1977; Pacala 1988) because fires sizes are typically far greater than propagule dispersal ranges. Thus regeneration depends on *in situ* seeds and there are apparently no species entirely dependent on *ex-situ* seeds.

From the plant's perspective, therefore, the general fire regime is predictable but the particular circumstances associated with each fire are unique (Kruger 1983; Cowling 1987; Bond & van Wilgen

1996).

1.3 Life-history theory

Ecological theories tend to deal with proximate explanations, those attempting to understand how the traits of an organism operate within its current habitat to enable the species to survive. Evolutionary theory seeks ultimate explanations, those attempting to understand how the organism has come to possess its present traits (Harper 1967; Willson 1983). Life-history theory attempts to bridge these two views by seeking explanations for the observed relationships between plant traits and demography under a given set of environmental (biotic and abiotic) constraints (Stearns 1976, 1977; Willson 1983; Cowling 1987).

Life-history theory attempts to provide coherent answers to the following question:

> *Given a particular environmental setting, how should an individual distribute its resources between reproduction and persistence to maximize its contribution to future generations?*

The central axiom of life-history theory is that organisms have finite resources with which to meet the competing, and often conflicting, demands of persistence (survival) and reproduction (Cody 1966; Law 1979; Stearns 1989). The issue of whether to allocate resources to survival or reproduction has received the most attention. It has been addressed from two points of view:

- the specific issue of whether to produce offspring just once (semelparity) or more than once during a lifespan (iteroparity).
- the general question of how to identify the reproductive schedule that gives the greatest fitness.

Much less attention has been given to how many young to produce at a time and whether and how far to disperse.

1.3.1 Semelparity and iteroparity

The life-histories of organisms can be divided into two groups based on reproductive episodes: those which have only one episode (semelparity) and those with more than one (iteroparity) (Cole 1954; Charnov & Schaffer 1973). Selection will favour iteroparity in populations with higher juvenile than adult mortality, decreasing offspring per crop and larger offspring; semelparity will be favoured in populations experiencing constant mortality rate for both juveniles and adults or an increase in mortality among adults (senescence), increasing offspring per crop and smaller offspring (Horn 1978). These patterns are self-reinforcing so, for example, once the increase in the number of offspring outweighs the

concomitant increase in adult mortality of an iteroparous plant (due to decreased investment in survival) - under a particular set of conditions - investment in reproduction will increase at the expense of parental survival until mortality is complete and the plant is semelparous. This explanation is consistent with Williams' (1957) hypothesis that senescence is the consequence of selection for increased reproduction at an early age even though this can reduce the lifespan.

1.4 Fires and plant demography in mediterranean shrubland communities

Fire-prone mediterranean shrublands have been the subject of a number of syntheses which have found substantial evidence of convergent evolution (Di Castri & Mooney 1973; Mooney and Conrad 1977; Specht 1979, 1981; Kruger *et al.* 1983; Keeley 1986; Cowling *et al.* 1994). These studies have concentrated on the effects of similar climates and dissimilar soil nutrient status in shaping community structure, life-form composition, plant physiognomy and ecophysiology and post-fire succession and recovery modes of plants in these shrublands. Initially, the effects of similarities and differences in fire regimes on plant demography and reproductive ecology were neglected but this has changed in recent years (Le Maitre & Midgley 1992; Keith & Bradstock 1994; Bond *et al.* 1995; Bond & van Wilgen 1996).

1.4.1 Seed-regenerating (seeding) Proteaceae

Studies of the demography of the dominant tall shrub species of the Proteaceae in Australian and Cape shrublands have identified many striking similarities between these phylogenetically unrelated species. These include: (a) most species regenerate only from seeds after fires (termed seeders; see Lamont *et al.* 1985; Le Maitre & Midgley 1992; Groom & Lamont 1996); and (b) many dominant species accumulate seeds in their canopies in persistent woody fruits - a trait known as serotiny (Lotan 1967) and found also in several pine species (Lamont *et al.* 1991b; Le Maitre & Midgley 1992; Dalaskalakou & Thanos 1996). There are also some striking differences: kwongan has many more serotinous sprouting species and many tall shrubs which sprout from epicormic buds; these sprouting species may dominate the overstorey and form closed communities unlike fynbos where *Protea nitida* is the only true epicormic sprouter and forms an open shrubland (Le Maitre & Midgley 1992).

1.4.2 Variability in recruitment

Although seeding Proteaceae are frequently important or dominant in fynbos communties, their densities can vary enormously both spatially and temporally.

Fire frequency

Changes in the frequency of fires can alter the composition of fynbos and kwongan communities primarily by changing the abundance of the tall shrubs of the Proteaceae (Bradstock & Myerscough 1981, 1988; Bond 1980, 1984; Van Wilgen 1981; Enright *et al.* 1996). When fires recur at intervals shorter than the time required for the plants to mature or accumulate adequate seed banks then the populations become extinct (Bradstock & Myerscough 1981; Van Wilgen 1981). When fire is excluded, deliberately or by chance, for long periods they begin to senesce and recruitment after fires at this stage can be poor (Bond 1980; Gill & McMahon 1986). At two sites in the Jonkershoek valley a second generation of seedlings became established without fire (Le Maitre 1992; Le Maitre & Botha 1994). These occurrences seem to be rare as regeneration between fires is thought to be prevented by seed predation by small mammals (Bond 1984; Breytenbach 1984). Studies on Proteaceae in Australian kwongan also have recorded recruitment in old stands (Gill & McMahon 1986; Bradstock & O'Connell 1988; Witkowski *et al.* 1991). These patterns differ from those recorded for seeders in chaparral where mortality rates are more or less constant (exponential), there is no evidence of senescence or an abrupt decline in fertility near the end of the lifespan (Montygierd-Lloyba & Keeley 1987; Zammit & Zedler 1992), and recruitment is absent in old stands (Keeley 1986; Zammit & Zedler 1992).

Fire season

Variations in the recruitment (number of seedlings per parent) of serotinous Proteaceae after fires in different seasons have been studied in considerable detail. The main factors are those which influence:

(1) The size of the seed banks, namely variation in the number of seeds stored on a plant because (a) only a few seed crops are retained on the plant (Jordaan 1949, 1965); or (b) pre-dispersal seed predators rapidly reduce the seed banks (Zammit & Hood 1986; Coetzee & Giliomee 1987; Witkowski *et al.* 1991; Wright 1994; Chapter 4); or (c) seeds decay fast (Van Staden 1978; Le Maitre 1990; Le Maitre & Botha 1991); or (d) seeds may be killed in the inflorescence by the heat of the fire (Midgely & Viviers 1990); or various combinations of these factors.

(2) The survival of seeds after dispersal: (a) the loss of viability and decay of seeds as they lie exposed to the harsh conditions on the soil surface during the summer after winter or spring fires compared with the short period of exposure after late-summer and autumn fires (Bond 1984; Cowling & Lamont 1987; Enright & Lamont 1989; Midgley 1989; Le Maitre & Botha 1991); and (b) seed predation by rodents between seed release and seed germination - the seeds are exposed to predation for longer after winter and spring fires than after summer and autumn fires (Bond 1984; Bond *et al.* 1984; Cowling & Lamont 1987; Le Maitre 1990; Botha & Le Maitre 1992; Chapter 5).

(3) The survival of seedlings: (a) high mortality of seedlings that become established in late-winter or

spring after fires at this time compared with seedlings that became established early in the winter after summer or autumn fires (Vogts 1982; Midgley *et al.* 1989; Chapter 5); or (b) the timing of onset and the amount of rainfall following the fire (Bradstock & Myerscough 1981; Specht 1981; Le Maitre 1987a; Lamont *et al.* 1991a; Bradstock & Bedward 1992; Richards & Lamont 1996).

1.5 Life-history theory and fire-prone environments

1.5.1 Differences from standard life-history

The demographic patterns and plant life-cycles in fire-prone environments described above have some characteristics which differ from the standard life-history models. These include:

Episodic recruitment

Life history theory has been developed by scientists working within a paradigm where, at least in theory, there is no delay between the production of seeds and the recruitment of seedlings. The classical iteroparous plant in life-history models has overlapping generations, continuous or regular recruitment and, generally, age or stage structured populations (Stearns 1976, 1977; Hilbert 1987). Seeders in fire-prone shrublands have non-overlapping generations, requiring adaptations to the normal lottery models (Laurie & Cowling 1994). Many plants in fire-prone systems have seeds which are only released, or cued to germinate, after fires (Hilbert 1987; Clark 1991). Reproduction is almost entirely restricted to the post-fire environment. Populations generally consist of single cohort of plants with the number of plants reaching a maximum after germination (during the first wet season following the fire) and then declining more or less continuously between fires (Clark 1991). The closest analogue for this life-history in the standard theory is that of the semelparous (annual) plant. Sprouters differ fundamentally from seeders in this respect as generations do overlap resulting in multi-cohort populations (Gill 1975; Keeley 1986; Bond 1987; Le Maitre 1992). Most sprouters recruit seedlings primarily after fires but some recruit new individuals almost exclusively between fires (Keeley 1986; Manders 1990; Le Maitre & Midgley 1992; Le Maitre 1992). This study concentrates on *Protea nitida* which recruits seedlings mainly after fires (Le Maitre 1992).

Seed banks and seed dormancy

Studies of the dynamics and implications of seed banks and seed dormancy have been limited largely to its role in annuals in spreading seed germination over several years to reduce the risk of extinction. In fynbos species the potential fecundity of a plant is influenced by the longevity of its seeds, either on the plant or in or on the soil, as this is a major determinant of the number of seeds accumulated at the time of the next fire. Cohen (1968) developed models which predicted the dynamics of seed banks of annuals but these are inappropriate for fire-prone environments because they are based on *risk-spreading*

germination (over several seasons) rather than *disturbance-cued* germination (Grubb 1988).

Exogenously caused mortality

Mortality schedules are considered to be a consequence of selective pressures for the optimal reproductive schedule based on the patterns in the reproductive value of the species (Williams 1957; Stearns 1976, 1977; Law 1979; Reznick 1988). They are, therefore, essentially *endogenously* determined by a trade-off between allocation to growth and maintenance versus reproductive output in favour of maximum fitness. But in a fire-prone system synchronous mortality in fires is *exogenous*, driven *inter alia* by the accumulation of fuel which is partially a biological process (Gill 1975; Walker 1981). This implies that the longevity of seeding plants should be such that they survive, either as seeds or as mature plants with seeds, until there is virtual certainty of a fire. On the other hand seeders have to ensure that they have produced seeds by the time a fire is likely to occur so there is also selective pressure for early reproduction. Thus there must be a relationship between the probability of a fire and the juvenile period of seed regenerating species (Clark 1991).

Biotic factors

In fire-prone shrublands there is strong evidence that biotic agents such as seed predators have been important selective factors in the evolution of reproductive traits such as serotiny, myrmecochory and mass flowering. Biotic and abiotic factors impose different selective pressures. While abiotic environments are generally relatively constant (at least at the scale of generation times) and so permit some optimisation of traits, biotic factors evolve along with the organisms, constantly changing the selective pressures and turning evolution into a race (Van Valen 1973; Harper 1977). An example for serotinous species is insect predation of seed in the persistent inflorescence. The costs of this are high because the nutrient costs of seeds are high and because a substantial seed bank is needed to buffer the adverse impacts of factors such as fires in an unfavourable season (Bond 1984; Bond *et al.* 1984) or fires which are followed by a delay in the rainfall or dry summers (Le Maitre 1987a).

These differences: delayed recruitment, discrete generations, seed dormancy, disturbance cued germination, exogenously driven mortality, clearly show that standard life-history theory cannot incorporate the life-histories of plants in fire-prone systems (Stohlgren and Rundel 1986; Bond 1987; Hilbert 1987; Grubb 1988; Clark 1991).

1.5.2 **Fire life-histories: sprouters and seeders**

Some studies have sought analogies in standard life-history theory for the patterns of traits of sprouters and seeders, and the evolution of seeders from sprouters. Because recruitment is effectively restricted to the immediate post-fire environment, seeders are analogous to semelparous organisms and sprouters

to iteroparous ones (Keeley 1986; Bond 1987; Bond and Van Wilgen 1996). Seeders must recruit enough seedlings to compensate for the seedling recruitment of the sprouters *and* the survival of established plants, if they are to have an evolutionary advantage. Expressed in mathematical form following Charnov & Schaffer's (1973) analysis (see Bond and van Wilgen 1996):

$$SB\_Sdr * NR\_Sdr > SB\_Spr * NR\_Spr + Spr\_survivors$$

(Spr = sprouter; Sdr = seeder; NR = net recruitment rate; SB = seed bank)

Thus, seeders can gain an advantage by producing more seeds, or by having longer-lived seeds (greater seed banks), seeds with a lower mortality during fires, or seedlings and juveniles with a higher survivorship (Bond 1987; see also Keeley 1986; Bond and van Wilgen 1996). The critical feature for sprouters is not survival *per se* but survival of seedlings and juveniles through fires until they, in turn, reach maturity. This may require many fire cycles (Bradstock & Myerscough 1988; Bradstock 1990; Le Maitre & Midgley 1992).

Clark (1991) adopted an alternative approach and developed life-history models which explicitly took into account the ways in which plant demography in fire-prone environments deviates from the assumptions of classical life-history discussed in the previous section. He assumed that:

- seeders (his type A) maximise the probability of being reproductively mature at the time of a fire, and
- that sprouters (his type B) maximise the number of reproductive episodes (fires) they experience during their reproductive lifespans.

Thus type-B (sprouting) plants have to trade-off fire survival against seed production over a series of fires. I examine these models in Chapter 6 where I test them using data on fire frequency distributions and plant maturation and mortality in seeders and a sprouting species.

1.6 Appropriate statistical models for cohort data

The analyses in Chapter 2 of this thesis involve statistical comparisons of cohort survival data. I examined a number of analyses of cohort data (e.g. Bishop *et al.* 1978; Law 1979, 1981; Leverich and Levin 1979; Angevine 1983; Mack and Pyke 1983; Bradstock and O'Connell 1988; Morris and Myerscough 1988) to determine what method to use when comparing survivorship between species and for different age ranges within species. In some of these studies mathematical functions were fitted to the data using standard least squares regression on (log-transformed) values. Regression techniques can be used to fit models to data on population trends, but, because the successive observations are not independent, the confidence limits cannot be validly derived and curves for different cohorts cannot be compared (Morris and Myerscough 1988; Prof. A. Van Laar pers. comm. 1988). In addition to this, the

survival of certain individuals beyond the last observation (right-censoring of the data) results in an underestimate of the life-spans of the survivors (Pyke and Thompson 1986). The study by Leverich and Levin (1979) is the only one I have found that used a life-table approach to analyze the life-history of a single cohort of plants. Kruger (1987) used the approach proposed by Bart and Robson (1982) but this has limitations as the Mayfield estimator assumes that a constant proportion of the population dies during each time interval (Dr L.G. Underhill pers. comm. 1987). In this study I followed Leverich and Levin (1979) who calculated daily mortality by dividing the mortality in an interval by the number of days in the interval, but using years as the unit for time.

1.7 Outline of the thesis

In the discussion above I briefly reviewed the demography of seeding shrubs and described the need for a logical approach to fynbos plant population dynamics which is based on testing life-history theory on field data. There are several key gaps in the current demographic data, for example the proportion of seeds which produce seedlings and how different factors influence this; the proportion of seedlings which reach maturity; the patterns of seed bank accumulation and how these differ between species. The studies in this thesis therefore were also directed towards collecting data to close these gaps as a step towards building complete demographic models.

Chapters 2 to 5 centre on seed bank dynamics and age-specific mortality mortality patterns. Several studies have provided data on age-specific mortality, seed banks and seed accumulation with increasing post-fire age in Australian *Banksia* species (for example Gill & McMahon 1986; Cowling et al. 1987; Bradstock & O'Connell 1988; Lamont & Barker 1988; Enright *et al.* 1996). But similar studies of Cape Proteaceae are lacking. There are no published studies on long-term mortality and studies of seed banks have typically examined a single age group (for example Bond 1995; Esler & Cowling 1990; Mustart & Cowling 1992a; Maze and Bond 1996). Only two studies have assessed the effects of stand density on seed banks in Cape Proteaceae, those of Esler & Cowling (1990) and Bond *et al.* (1995). Chapters two and three of this thesis analyse data on reproductive maturation on seed banks at different ages to answer the following questions:

(1) What are the patterns in mortality during the lifetime of serotinous Proteaceae and is there evidence for programmed senescence?

(2) What are the patterns of reproductive maturation and seed bank accumulation in Proteaceae?

(3) How does stand density influence flowering and seed bank accumulation in co-occurring *Protea neriifolia* and *P. repens*?

There have been a number of studies of the impacts of pre-dispersal predation by insects of seed banks of Cape Proteaceae by insects (e.g. Myburgh *et al.* 1974; Coetzee & Gilliomee 1987). Studies by Wright

(1994) and Mustart *et al.* (1995) found evidence that low seed-set and distribution of seeds within the inflorescence may influence seed predation levels. This study examined seed predation patterns in two occurring species: *Protea neriifolia* - with low seed set, and *P. repens* - with relatively high seed set to answer the following question:
(4) What impacts do pre-dispersal seed predators have on seed bank dynamics, and do patterns in seed set suggest that species differ in their responses to seed predation?

A number of studies have examined net recruitment (seedlings per parent) following fires in different seasons (e.g. Bond *et al.*1984; Cowling & Lamont 1987; Lamont *et al.* 1991a) but only one has examined the effect of the timing of seed germination on subsequent seedling survival (Midgley *et al.* 1989). Chapter 5 takes this study further and sought to answer the following question:
(5) How does the temporal distribution of rainfall influence seed germination, and seedling establishment and mortality during the first summer drought?

Life-history provides a framework for understanding all these patterns, especially the way in which mortality, longevity and age at first reproduction can be related to the distribution of the occurrence of fires in time in fynbos environments. As discussed earlier, many of the assumptions underlying classical life history are violated in fire-prone environments. A new set of life-history models are needed and one has been proposed by Clark (1991). In Chapter 6 I address the question:
(6) Do Clark's (1991) hypotheses about the relationship between fire frequency distributions and the age at first reproduction (juvenile periods) and reproductive lifespans of seeding and sprouting species hold for fynbos species?

In the final section I summarise the current knowledge of the demography and life-histories of the Proteaceae and suggest some areas for further research.

Chapter 2: Mortality, reproductive development and seed bank dynamics of *Leucadendron xanthoconus*, *Protea neriifolia* and *Protea lacticolor* (Proteaceae) at Jakkalsrivier, south-western Cape[1] (co-author CA Jones)

2.1 Abstract

This paper examines patterns in the mortality rates, plant maturation and seed bank accumulation of *Protea neriifolia* R. Br., *P. lacticolor* Salisb. and *Leucadendron xanthoconus* (Kuntze) K. Schum., non-sprouting, serotinous members of the Cape Proteaceae, over a period of 10 years. Populations in an area burnt twice at 10-year intervals and last burnt in 1958 (old sites) were monitored. Three *P. lacticolor* sites were selected within the area burnt at 10 year intervals to test the influence of a moisture gradient on plant growth and development. Mortality and reproductive development were monitored over a period of 10 years. No data were available for mortality during the first summer. The effective annual mortality rates were highest during the second summer after establishment, ranging from 1.5 % (*P. lacticolor* wet site) to 16 % (*L. xanthoconus*). The mortality rates from 1-10 years of age varied from 13.1 % in *P. neriifolia* to 40.0 % in *L. xanthoconus*, which was significantly lower than that from 21-30 years of 53% for *P. lacticolor* and 61% for *L. xanthoconus*. The percentage of mature plants in flower in a given year declined with age though the decline was more gradual for the plants on the old sites. There was no evidence of a consistent decrease in the number of full seeds per inflorescence with increasing inflorescence age in any of the species. The youngest seed crop did, however, comprise 46-85 % of the total seed bank in all three species. Rodents and baboons removed 50-90% of the inflorescences of *Protea neriifolia* and *Protea lacticolor* shrubs at the dry and moist sites but no damage was recorded for *Leucadendron xanthoconus*. There is no evidence that populations of these three species have declined when burnt at 10 year intervals but fires at five year intervals have eliminated all three species. Seed banks of *L. xanthoconus* and *P. neriifolia* appear to be adequate at the age of 10 years but those of *P. lacticolor* were low and could lead to extinction.

2.2 Introduction

Tall shrubs in the Proteaceae which store their seeds in the canopy (a trait known as serotiny, Lotan 1967) dominate many communities in the fynbos shrublands of the Cape Province, South Africa. Fire

---

[1]: Publication status: DC Le Maitre & C A Jones in preparation. Mortality, reproductive development and seed bank dynamics of *Leucadendron xanthoconus, Protea neriifolia* and *Protea lacticolor* (Proteaceae) at Jakkalsrivier, south-western Cape.

is a key element in the life-cycles of fynbos plants and most species depend on fire for regeneration. Many species are killed by fire and rely entirely on their seeds for survival. The seeds are apparently well protected from fire but regeneration success is influenced by many factors including pre-fire seed banks, fire frequency, exposure on the soil surface and seed predation by small mammals (Jordaan 1965; Bond 1984; Bond et al. 1984; Bond and Breytenbach 1985; Midgley 1989; Esler and Cowling 1990; Le Maitre & Midgley 1992; Botha & Le Maitre 1992; Bond & Van Wilgen 1996).

The structure of the plant community is a result of past events rather than the present conditions (Bond *et al.* 1984). Pre-fire records of population structure, reproductive development and seed bank dynamics are, therefore, important for predicting post-fire regeneration. The success of post-fire recruitment is determined by a number of factors. These include:
i) the time to reproductive maturity which is critical in terms of fire frequency (Clark 1991);
ii) post-fire seedling establishment which may be affected by climate, predators and intensity and season of fire. Maximum seedling recruitment occurs after late summer and early autumn fires and recruitment is usually poor after winter or spring fires (Bond 1984, Van Wilgen & Viviers 1985); and
iii) size of pre-fire seed banks (Jordaan 1965; Bond et al. 1984; Bond 1985; Bradstock & O'Connell 1988; Midgley 1989; Bond *et al.* 1995).

Quite a large body of information on the seedbank dynamics of serotinous Cape Proteaceae has been accumulated since the pioneering studies by Jordaan (1949), Horn (1962) and Lombaard (1971), including comparisons of similar species (Mustart *et al.* 1994; Maze & Bond 1996). Accumulated seeds form a buffer against fluctuations in annual seed output and against seasonal variations due to seed predation and loss of viability of seed in the capitulum (Bond 1985; Coetzee & Giliomee 1987). In senescent fynbos, seed supplies may limit regeneration after fire (Bond 1980) while in mature vegetation seed predation, stand density and other factors are important (Bond 1984; Bond *et al.* 1995; Maze & Bond 1996).

We studied populations of *L. xanthoconus*, *P. neriifolia* and *P. lacticolor* to answer the following questions:
(i) Do mortality rates increase significantly with increasing age?
(ii) How rapidly do the plants mature?
(iii) How rapidly do the plants accumulate seed banks?
(iv) What factors influence the accumulation of seed banks?

The results of these analyses are compared with data from studies of Cape and Australian Proteaceae.

2.3 Study site

The study was conducted in the Jakkalsrivier catchment in the Groenland mountains about 20 km east of Grabouw (34°09'S, 19°09'E) in the south-western Cape. The catchment has been described in detail by Kruger (1974, 1987). The study sites are situated at an altitude of about 800 m on a south to south-east facing slope. The mean annual rainfall is about 860 mm, 65 % percent falling from April to September. The climate is mild with mean daily maximum 23.2°C and minimum of 12.0°C in January and 14.1 and 6.3°C respectively in July. The soils of the study sites are derived from shales and have higher nutrient levels than sandstone derived soils (Kruger 1987). The plant community is a dense proteoid shrubland (30-60 000 plants per ha) dominated by *Leucadendron xanthoconus* on dry sites and *Protea lacticolor* on moister sites near streamlines.

The catchment has been used for studies of hydrological responses to fire (Plathe & Van der Zel 1969). It was divided into two catchments, one burnt regularly and one protected from fire since 1958. The regularly burnt catchment was divided into sub-catchments which were burnt at five and ten year intervals in spring or autumn. The sample sites were located in a sub-catchment burnt in autumn at ten year intervals and in the protected catchment (hereafter called the 'old' site).

2.4 Methods

Three species in the Proteaceae, *Protea lacticolor*, *P. neriifolia* and *Leucadendron xanthoconus*, were sampled in the area burnt at 10-year intervals (hereafter called young). Additional sample sites for *P. lacticolor* and *L. xanthoconus* were located in the area protected from fire since 1958. Samples of 100 individuals were selected using the Wandering Quarter method of Catana (1963) and marked with numbered wire stakes. The young *P. lacticolor* samples were replicated over a moisture gradient - a wet site along a stream line, a moist site and a dry rocky site on colluvium below a scarp - to see how this influenced plant growth and development from seedlings (2nd year after fire) to 10 years of age. All three *P. lacticolor* sites were located within 100 m of each other. The old populations were located in a moist site with similar vegetation. These populations provided data on mortality from 22 to 30 years of age. Mortality rates at different ages were analysed using a Logrank test (Hutchings *et al.* 1991).

The maturation, flowering and number of inflorescences of the tagged plants was recorded at each survey. Notes were made, in 1988, of rodent (probably *Otomys* spp.) or baboon (*Papio ursinus*) damage to the plants in the form of chewed or broken off shoots and inflorescences. Seed bearing

inflorescences were collected in March 1990 from a random sample of 30 plants (except for *L. xanthoconus* where only 7 females occurred in the sample) and divided into age classes. The inflorescences were dried at 30°C and the seeds were sorted and cut open to determine the number with firm, white embryos, hereafter termed full seeds.

2.5 Results

2.5.1 *Plant mortality and reproductive development*

There was no evidence of a marked trend in the annual mortality rate (the fraction dying per unit time [q_x]) of young *L. xanthoconus* (Table 2.1). The highest annual mortality rate was recorded between 1.45 and 2.04 years of age, during the second summer after the fire, and the mortality rate was also high between four and five years of age when the first plants matured. Juvenile (sexually immature) plants declined from 66 % of the sample at five years to 5 % at 10 years of age. The mean annual mortality rate of 9.0 % (mean q_x = 0.090, SD = 0.032) for the old plants was significantly higher than the 6.1 % of the young plants (mean q_x = 0.061 SD = 0.045; Logrank value = 6.81, $Chi^2_{1DF\ P=0.01}$ = 6.63). The mortality rates of the old males (75.9 %) were significantly higher than those of the females (51.9 %; Logrank value = 6.81, $Chi^2_{1DF\ P=0.01}$ = 6.63). There was little indication that the annual mortality rate increased with age in the old plants although it was high from 27-30 years of age. The mortality rate of both young and old plants was also high during the 1981-1982 period - 1.45 to 2.04 and 22.44 to 23.12 years of age, respectively. Mortality rates of young *L. xanthoconus* plants were significantly higher than those of young *P. neriifolia* (Logrank value = 16.29, $Chi^2_{1DF\ P=0.01}$ = 6.63) and young *P. lacticolor* (Logrank value = 3.72, $Chi^2_{1DF\ P=0.10}$ = 2.71). Mortality rates of old *L. xanthoconus* and *P. lacticolor* did not differ significantly (Logrank value = 0.45).

The percentage of female *L. xanthoconus* plants producing inflorescences decreased from 80 % of the mature plants at five years to 64 % at 10 years of age (Table 2.1). One female plant developed buds but aborted its inflorescences at five years of age. Flowering of male *L. xanthoconus* plants was not always recorded but where flowering was recorded, no plants had skipped a flowering season.

The plants bore few inflorescences and inflorescence production per shrub changed little from eight to 10 years of age (Table 2.1). At 10 years of age the sample was dominated by male plants, 3.07 males/female, little changed from the 4.0 males per female when the plants first matured. The sex ratio of the 21 year old plants was nearly equal, 0.92 males per female, but by the age of 31 years this had decreased to 0.58 males per female.

TABLE 2.1. Mortality rates and reproductive development of populations of *Leucadendron xanthoconus*. No data were available on inflorescence production in the old population. Ages were calculated using 15 June of the winter after the fire as the mean date of seed germination after fires. Mature plants of *L. xanthoconus* are given as number female/male and number in flower (female only).

Species	Age (yrs)	Number alive	Annual mortality rate (q_x)	Number of			Number of inflorescences per flowering plant	
				juvenile plants	mature plants	mature plants in flower	mean±SD	range
L. xanthoconus	0.91	100	-	100	0			
(last fire 1980)	1.45	98	0.037	98	0			
	2.04	89	0.157	89	0			
	2.86	88	0.014	88	0			
	4.07	81	0.066	81	0			
	5.18	73	0.089	48	5/20	4	1.00±0.00	1
	7.75	65	0.043	10	14/41	13	1.62±0.65	1-3
	8.83	63	0.029	5	15/43	14	2.00±0.88	1-3
	9.69	60	0.055	3	14/43	9	1.67±0.50	1-2
L. xanthoconus	21.45	100	-	0	52/48			
(old	22.44	95	0.050	0	50/45			
catchment)	23.12	88	0.109	0	48/40			
	23.87	82	0.092	0	46/36			
	25.07	74	0.081	0	40/34			
	26.18	66	0.097	0	39/27			
	28.75	52	0.083	0	33/19			
	29.82	43	0.161	0	29/14			
	30.69	39	0.108	0	25/14			

Table 2.2. Mortality rates and reproductive development of *Protea neriifolia*. The initial sample was 100 plants but a *P. lacticolor* seedling was inadvertently included and it was excluded from the analyses. Ages are calculated using 15 June 1980 as the mean date of seed germination after a fire in March 1980.

Species	Age (yrs)	Number alive	Annual mortality rate (q_x)	Number of			Number of inflorescences per flowering plant	
				juvenile plants	mature plants	mature plants in flower	mean±SD	range
P. neriifolia	0.91	99	-	99	0			
	1.45	99	0.000	99	0			
	2.04	93	0.103	93	0			
	2.86	92	0.013	92	0			
	4.02	88	0.038	84	4	4	1.00±0.00	1
	5.18	87	0.010	74	13	9	1.00±0.00	1
	7.82	87	0.000	20	67	50	1.90±1.31	1-8
	8.83	87	0.000	13	74	42	2.36±1.56	1-6
	9.69	86	0.013	11	75	46	2.39±1.64	1-7

The annual mortality rates of *Protea neriifolia* varied little and, like *L. xanthoconus*, was highest between 1.45 and 2.04 years of age (Table 2.2). The mean annual mortality rate from one to 10 years of age (mean $q_x = 0.022$, SD = 0.035) was low and there were three intervals when no plants died. The proportion of juvenile plants declined from 95 % at four years of age to 13 % at 10 years of age. The proportion of mature plants which flowered again in a given year decreased to 69% at five years to 57 % at nine years of age. Mean inflorescence production per shrub increased with increasing age, but the range in the number of inflorescences produced per plant changed little from eight to 10 years of age. There was little evidence of a consistent pattern in the annual mortality rates of young *P. lacticolor* plants at any of the four sites (Table 2.3), but the rates differed significantly between sites (Logrank value = 6.90, $Chi^2_{2DF\ P=0.05} = 5.99$), being lowest at the dry site (mean $q_x = 0.030$ SD = 0.026). The mean mortality rates of old *P. lacticolor* plants (mean $q_x = 0.074$ SD = 0.039) were significantly higher than the young plants (Logrank value = 19.89, $Chi^2_{1DF\ P=0.01} = 6.64$).

Plants in the *P. lacticolor* populations at the dry and moist sites matured at four years of age compared with five years of age at the wet site. At five years of age, 27 % of the plants at the moist site were mature compared with 14 % at the dry site. At 10 years of age, the corresponding values were 89 and 77 % while only 73 % of the wet site population had matured. The percentage of mature plants in flower in the younger samples varied from 50 to 83 % and was about the same as the old plants. In the last survey (1990), the percentage of mature *P. lacticolor* plants in flower varied from 44 % (moist site) to 59 % (wet site) compared with 81 % of the thirty-one year old plants. Plants at

the moist site produced more inflorescences per year than those at the dry and wet sites but the 31 year old plants bore many more inflorescences.

2.5.2 *Reproductive status in 1990*

The number of flowering seasons of mature plants of all the species at 10 years of age was similar (Table 2.4). *Protea lacticolor* had the highest percentage of immature plants (27 %). None of the female *Leucadendron xanthoconus* plants had six flowering seasons.

Less than half the populations had three or more flowering seasons with the highest being *Protea lacticolor* at the wet site (47%) and the lowest *L. xanthoconus* (31%). The number of seed bearing inflorescences increased each year except for *L. xanthoconus* which bore fewer inflorescences in 1989 (Table 2.5). The absence of inflorescences of *L. xanthoconus* from 1990 is due to the timing of its flowering in mid-winter so that inflorescences for 1990 had not yet developed at the time of sampling in February 1990. *Protea lacticolor* plants at the moist site generally bore the most inflorescences followed by plants from the dry and wet sites.

TABLE 2.3. Mortality rates and reproductive development of populations of *Protea lacticolor*. The initial sample was 100 plants but some *Protea neriifolia* seedlings were inadvertently included. These individuals were excluded from the analyses. Ages are calculated using 15 June 1980 as the mean date of seed germination after a fire in March 1980.

Species	Age (yrs)	Number alive	Annual mortality rate (q_x)	Number of			Number of inflorescences per flowering plant	
				juvenile plants	mature plants	mature plants in flower	mean±SD	range
P. lacticolor	1.45	92	-	92	0			
(dry site)	2.04	91	0.018	91	0			
	2.86	87	0.054	87	0			
	4.07	84	0.028	82	2	2	1.00±0.00	1
	5.18	84	0.000	72	12	10	1.10±0.32	1-2
	7.84	75	0.041	34	41	29	2.62±2.11	1-9
	8.84	70	0.067	23	48	33	2.39±2.19	1-8
	9.69	70	0.000	19	51	36	2.11±1.62	1-7
P. lacticolor	0.91	99	-	99	0			
(moist site)	1.44	97	0.038	97	0			
	2.12	94	0.045	94	0			
	2.86	93	0.014	93	0			
	4.07	86	0.058	79	7	7	1.00±0.00	1
	5.18	85	0.009	62	23	17	1.35±0.79	1-6
	7.82	69	0.061	24	45	34	3.02±3.07	1-15
	8.84	63	0.060	13	50	33	2.55±3.01	1-17
	9.69	62	0.012	7	55	27	2.78±2.95	1-12
P. lacticolor	0.91	100	-	100	0			
(wet site)	1.44	97	0.056	97	0			
	2.12	96	0.015	96	0			
	2.86	90	0.084	90	0			
	4.07	88	0.018	88	0			
	5.18	87	0.010	75	12	12	1.25±0.62	1-3
	7.84	81	0.026	41	40	27	3.02±3.07	1-6
	8.86	75	0.073	28	47	30	2.50±1.85	1-8
	9.69	69	0.096	16	53	40	2.68±2.10	1-11
P. lacticolor	22.45	100	-	0	100	no data		
(old	23.19	94	0.081	0	94	no data		
catchment)	23.87	94	0.000	0	94	81		
	25.07	81	0.114	0	81	78		
	26.54	69	0.101	0	69	53		
	28.88	53	0.099	0	53	50		
	29.86	49	0.077	0	49	44		
	30.69	47	0.049	0	47	38	13.00±9.46	1-30

Table 2.4. Frequency distribution of the number of flowering seasons of mature (9.6 year old) female *Leucadendron xanthoconus* and mature *Protea neriifolia* and *P. lacticolor* plants in March 1990. Percentages for *L. xanthoconus* were calculated for females only and assume that the remaining juveniles are all females.

Species	Percentage with the given number of flowering seasons						
	0	1	2	3	4	5	6
L. xanthoconus	23	15	31	8	15	8	0
P. neriifolia	13	25	20	15	19	7	1
P. lacticolor (dry site)	27	13	23	11	11	6	9
P. lacticolor (moist site)	11	18	29	13	15	14	0
P. lacticolor (wet site)	23	20	18	7	17	9	6

Table 2.5. The net number of seed bearing inflorescences from different years on mature (9.69 year old) shrubs of three Proteaceae species at Jakkalsrivier in March 1990. *Protea lacticolor* samples were separated according to sites. The number of shrubs with inflorescences in each year class is given in parentheses.

Species	Mean number of inflorescences						Range
	1985	1986	1987	1988	1989	1990	in 1990
Leucadendron xanthoconus	0	2.00 (1)	2.67 (3)	2.50 (4)	1.60 (5)	-	-
Protea neriifolia	1.00 (2)	2.00 (1)	1.50 (2)	2.12 (17)	2.00 (12)	2.06 (17)	1-5
Protea lacticolor - dry	0	0	2.00 (1)	0 (0)	2.94 (16)	3.00 (11)	1-10
Protea lacticolor - moist	0	0	1.25 (4)	2.00 (10)	2.79 (19)	3.27 (11)	1-12
Protea lacticolor - wet	0	0	1.00 (4)	1.63 (8)	1.38 (8)	2.67 (18)	1-8

Table 2.6. Seed banks of three mature (9.69 year old) Proteaceae species at Jakkalsrivier in February 1990. The *Protea* species' inflorescences from the 1990 season did not contain mature seeds at the time of sampling. See Table 2.5 for details of inflorescence production.

Species	Seeds per inflorescence (mean±SD) (total inflorescences per crop)					Total seeds per shrub (number of shrubs)	
	1985	1986	1987	1988	1989	mean±SD	range
Leucadendron xanthoconus	0	0.00 (2)	0.00 (8)	17.8±5.75 (10)	15.37±4.49 (8)	38.67±22.33 (6)	16-69
Protea neriifolia	0.00 (2)	18.50 (2)	0.00 (3)	9.09±9.11 (36)	12.75±10.04 (24)	33.15±31.13 (20)	1-102
Protea lacticolor - dry	0	0	2.00 (2)	0.00 (0)	2.26±2.21 (47)	10.50±7.91 (12)	1-28
Protea lacticolor - moist	0	0	2.13±2.95 (5)	4.49±5.52 (20)	1.91±1.41 (53)	13.18±17.35 (11)	1-67
Protea lacticolor - wet	0	0	4.75±6.18 (4)	0.75±1.39 (13)	2.38±2.38 (11)	5.78±4.44 (9)	1-15

Table 2.7. The influence of inflorescence removal by small mammals and baboons on the number of inflorescences on shrubs of two *Protea* species which flowered during the 1985 to 1987 flowering seasons.

	Statistic	1985 total	1985 removed	1986 total	1986 removed	1987 total	1987 removed
P. neriifolia	number of shrubs	9	0	16	12	35	7
	number of inflor.	9	0	21	18	53	10
P. lacticolor (dry site)	number of shrubs	10	0	18	11	29	4
	number of inflor.	11	0	44	31	77	39
P. lacticolor (moist site)	number of shrubs	17	3	13	5	29	5
	number of inflor.	41	3	66	7	70	9
P. lacticolor (wet site)	number of shrubs	11	3	16	13	27	13
	number of inflor.	14	3	37	34	61	42

The number of seeds per inflorescence did not show a distinct decline with increasing age in any of the species (Table 2.6). *Leucadendron xanthoconus* inflorescences from the 1986 and 1987 flowering seasons did not contain any full seeds nor did the *P. neriifolia* inflorescences from the 1985 and 1987 flowering seasons. *Leucadendron xanthoconus* plants had the largest seed banks followed by *P. neriifolia*. *Protea lacticolor* shrubs from the moist site had more seeds than those from the dry site and both had substantially more than plants from the wet site.

The number of inflorescences that had been chewed off by small mammals or broken off by baboons by the time of the 1988 survey varied among and within species. No inflorescences of *L. xanthoconus* had been chewed or broken off. Nine *Protea neriifolia* shrubs had lost their only inflorescence from the 1985 season and 86 % of the 1987 inflorescences had been removed (Table 2.7). At the dry site, no inflorescences of *Protea lacticolor* from the 1985 season had been removed but losses from the 1986 and 1987 crops were high (70 and 51 % respectively). Losses at the wet site were also high, 92 % of the 1986 and 59 % of the 1987 season's production. The lowest losses were recorded at the moist site and ranged from 7 % of the 1985 to 13 % of the 1987 crop.

2.6 Discussion

2.6.1 *Plant Mortality*

Mortality rates of Cape Proteaceae during the first and second summers after fires range from 7-20 % (Midgley 1988; Midgley et al. 1989; Le Maitre 1992) but can reach 45% (Maze & Bond 1996). The lower rates are similar to the effective annual mortality rates (annual q_x) recorded during the second summer in this study which ranged from 1.5 % (*P. lacticolor* wet site) to 16 % (*L. xanthoconus*). Mortality rates during the first summer were not recorded in this study because surveys began 15 months after the fire and about 12 months after seed germination began. The mortality rates of *Pinus halepensis* seedlings also decreased from the first to the second and subsequent summers (Thanos et al. 1996.)

The design of the samples in this study does not allow for an analysis of the influence of stand density on the observed mortality rates in *P. lacticolor*. The dry site had the lowest and the wet site the highest density (and most dense growth), but Kruger (1987) did not find evidence of density dependent mortality at the same site in the previous fire-cycle despite the high densities of 30-60 000 plants per ha. The mortality rates of young plants after the second summer were substantially lower than those of *P. neriifolia* at a site in Swartboskloof where the 99.8 % of the plants died between 1.5 and 12.6 years of age, but this appears to be unusually high (Le Maitre 1992). *Banksia ornata* may also experience high mortality rates with 99.5 % of

the plants dying between 1 and 11 years of age (Gill & McMahon 1986). The half-lives (time to 50 % mortality) of *Banksia ericifolia* and *Petrophile pulchella* varied from 0.1 to more than 3.0 years (Bradstock & O'Connell 1988), much shorter than those recorded in this study. There is no obvious explanation for the lower mortality rates of young established plants at Jakkalsrivier, and possibly generally in fynbos. The mortality rate of *Banksia ornata* seems to relatively constant throughout its lifespan (Gill & McMahon 1986) a pattern which is closer similar to that observed in *Orothamnus zeyheri* than in *Protea neriifolia* (Boucher 1981; Le Maitre & Midgley 1992; Chapter 6).

There is some evidence that the mortality rate of proteas increases with age (Kruger & Bigalke 1984). There was no evidence of a marked increase in the mortality rate from 21-31 years of age in *L. xanthoconus* or *P. lacticolor* but the mean annual mortality rates from 21-31 years were significantly higher than those from 1-10 years of age (Tables 2.1-2.3, Logrank test $p < 0.01$). Other studies have found that the mortality rates of mature, seed regenerating proteas and banksias increases with age (Kruger and Bigalke 1984; Bradstock 1990; Kruger 1987; Zammit & Westoby 1987; Le Maitre 1992), but this is the first to show a statistically significant increase. Overall, the mortality rates in Cape proteas appear to be high during the first and second summers, low from then until maturity and thereafter slowly increasing with age. There does not seem to be a well defined onset of senescence, the classic type I mortality curve of Pearl (1927), but just a steady increase in the annual rate. Loehle (1988) argues that, in plants, investment in the durable wood required for longevity can only be at the cost of delayed reproductive maturation and conversely that early reproduction is at the expanse of durable wood. Loehle's hypothesis is consistent with Williams (1957) argument that senescence is the result of increased investment in early reproduction and a concomitant reduction in the lifespan rather than physiological degradation at the cellular level or activation of deleterious genes (see Bell 1984). In seeding Proteaceae the cost of early reproduction appears to be manifested as a decreased investment in the strength or durability, or both, of the wood of its branches and stems with the result that senescence is marked by increasing breakages (Bond 1980; Gill & McMahon 1986; Witkowski *et al.* 1990; Burgman & Lamont 1992) - the shrubs literally fall apart. This does not happen to the much longer lived *Protea nitida* although branch die-back has been observed in 28 year-old plants of the lignotuberous sprouter *Leucadendron salignum* (Le Maitre pers. obs.).

2.6.2 *Reproductive development*

The age at first flowering of all three species was four to five years. The one-year delay in maturation of *P. lacticolor* at the wet site, compared with the dry site, may have been due to higher densities at the wet site but this could not be tested because of the sampling technique. Le Maitre (1992) found that a *P. neriifolia* population in Swartboskloof also matured at four years of age. This is shorter than the

juvenile period of some other Cape Proteaceae of 6 years (Le Maitre 1987b), but similar to the juvenile periods of Australian Proteaceae which first flower at four to five years of age (Gill & McMahon 1986; Bradstock & O'Connell 1988). Populations of obligate seed regenerating plants are especially vulnerable during the first few years because a fire during this period can cause the extinction of a population or even a species (Gill & McMahon 1986; Midgley 1989; Le Maitre 1987b). Populations of all three species have been eliminated in sub-catchments burnt at 5-year intervals. There have been no studies of the factors (e.g. size) which influence the duration of the juvenile period in Cape Proteaceae. *Protea neriifolia* plants were taller and had a higher biomass than *P. lacticolor* and *L. xanthoconus* plants of the same age (Kruger 1987; Le Maitre unpublished data) but matured at the same age as *P. lacticolor* (dry site) plants (Tables 2.2 & 2.3). *Protea lacticolor* plants on the dry site were shorter but had a similar biomass to plants on the wet site (Kruger 1987, Le Maitre unpublished data), but plants on the wet site first matured a year later. This suggests that, even within a species, sexual maturation is not strictly related to size.

The percentage of mature plants in flower in a given year declined with age though the decline was more gradual for the plants on the old sites. Bradstock & O'Connell (1988) also found that the proportion of mature *Banksia ericifolia* shrubs producing cones declined with age. The tendency to skip flowering seasons has also been noted in other Cape Proteaceae (Kruger & Lamb 1979; Le Maitre *et al.* 1991).

Kruger and Lamb (1979) allowed for the skipped flowering seasons in their rule-of-thumb that the minimum age at which a population could be burnt was when at least 50 % of the population had flowered for three or more years. Skipping of flowering seasons resulted in less than half the populations (42 %) of all three species having flowered for three or more times at an age of 10 years. This is lower than the 30.3 % which had flowered for three or more years in an eight year old *P. neriifolia* population in Swartboskloof (Le Maitre 1992). *L. xanthoconus* had the lowest proportion which had flowered for three or more seasons while *P. neriifolia* and *P. lacticolor* on the moist site had the highest. A similar pattern has also been found in populations of other serotinous Proteaceae where few plants had flowered in every possible season and most plants had only flowered for one to two seasons (Lombaard 1971; Le Maitre 1987b).

Mean annual inflorescence production of *P. neriifolia* increased with increasing age but was almost constant in *L. xanthoconus* (Table 2.1) and *P. lacticolor*. The highest annual inflorescence production of 13 per shrub was recorded in 31 year old *P. lacticolor* shrubs. Evidence from other studies on proteas indicate the same increase in inflorescence production with age (Esler & Cowling 1990; Chapter 3). Annual inflorescence production also increased with age in *Banksia* species but there were marked

fluctuations between successive years (Specht *et al.* 1958; Cowling *et al.* 1987; Bradstock & O'Connell 1988). Esler & Cowling (1990) found that for 16 year old *P. lepidocarpodendron*, the mean number of cones per plant ranged from 16.5 in dense stands to 171.2 in sparse stands. The mean annual inflorescence production per plant for 18 to 30 year old shrubs of the Proteaceae ranged from 4.0-33.7 (Bond 1985). Inflorescence production by the species in this study fell within this range where stand densities ranged from 30-60 000 plants per hectare (Kruger 1987).

2.6.3 *Seed bank dynamics*

There was no evidence of a consistent decrease in the number of full seeds per inflorescence with increasing inflorescence age in any of the species. These findings differed markedly from another study of *P. neriifolia* which found a significant decline in the number of full seeds per inflorescence with increasing inflorescence age (Le Maitre unpubl. data). The number of seeds per inflorescence also decreased with increasing inflorescence age in other Cape Proteaceae (Lombaard 1971; Bond 1985), partly because of seed predation by insects (Coetzee & Giliomee 1987; Mustart *et al.* 1994).

Leucadendron xanthoconus had the highest number of seeds per plant. *Protea lacticolor* shrubs at the moist site had more seeds than those at the dry and wet sites. The seed banks of *L. xanthoconus* and *P. neriifolia* compare favourably with those for samples of the same species at the same site and at the same age (Table 2.8, Kruger 1987). The seed banks of *P. lacticolor* in 1990 were however, considerably lower than those recorded by Kruger (1987). The seed banks of *P. neriifolia* are also similar to those for an eight year old population in Swartboskloof (Le Maitre 1992). Serotiny is weak in the Cape Proteaceae in comparison to strongly serotinous Banksias and viable seed is seldom stored more than four to six years (Bond 1985; Cowling et al. 1987). The youngest seed crop comprised 46-85 % of the total seed bank in all three species, which is comparable to that of other Cape Proteaceae and *Banksia* species.

A large proportion of the stored seed reserves of serotinous Proteaceae is destroyed by insects (Zammit & Hood 1986; Coetzee & Giliomee 1987) and baboons and rodents also remove inflorescences (Breytenbach 1982). In this study, up to 90 % of the mature inflorescences of *P. neriifolia* and *P. lacticolor* were removed by rodents and baboons. However, no inflorescences of *L. xanthoconus* were removed. The removals were sporadic but had a significant impact on the seed banks. This form of predation could lead to a delay in the build-up of an adequate seed reserve. Cockatoos can have a similar impact on seed reserves in several *Banksia* species (Lamont *et al.* 1985; Witkowski *et al.* 1991).

TABLE 2.8. Comparison with data for the same species at the same site by Kruger 1987.

Species	Stand age (years)	Seeds per plant		Source
		Current crop	Total	
L. xanthoconus	9	20.5	38.7	This study
L. xanthoconus	10	-	44	Kruger (1987)
L. xanthoconus	22	-	279	Kruger (1987)
P. neriifolia	9	15.3	33.2	This study
P. neriifolia	10	-	20	Kruger (1987)
P. neriifolia	22	-	44.3	Kruger (1987)
P. neriifolia	7	26.8	53.4	Le Maitre (1992)
P. neriifolia	12	22.6	34.3	Le Maitre (1992)
P. lacticolor (dry)	9	8.9	10.5	This study
P. lacticolor (moist)	9	9.2	13.2	This study
P. lacticolor (wet)	9	2.9	5.8	This study
P. lacticolor (dry)	10	-	38.6	Kruger (1987)
P. lacticolor (moist)	10	-	48.8	Kruger (1987)
P. lacticolor (intermed.)	22	-	372	Kruger (1987)

The populations of these species are situated in vegetation that has been burnt twice at intervals of 10 years and there is no evidence that the numbers have declined as a result of this fire regime. Populations of these species in adjacent areas which have been burnt every five years have been eliminated. Data on the number of seedlings per seed are sparse. *P. neriifolia* in Swartboskloof produced about 0.27 established seedlings per seed (Le Maitre 1992) while Maze & Bond (1996) recorded 0.46 and 0.57 seedlings per seed for *P. repens* and *P. neriifolia* respectively. In *Banksia* species the number of seedlings per seed ranged from 0.01 to 0.44 with a mean of 0.17 (Cowling et al. 1987; Bradstock & O'Connell 1988; Lamont & Barker 1988; Enright & Lamont 1989). Using a ratio of 0.2 seedlings per seed this gives a seedling recruitment of 7.7 for *L. xanthoconus*, 6.6 for *P. neriifolia* and 2.1, 2.6 and 1.2 for *P. lacticolor* on the dry, wet and moist sites respectively. Bond (1989) has suggested that the probability of population extinction is high if the number of seedlings per parent is less than four. The probability, therefore, of population extinction in the event of a fire is low for both *L. xanthoconus* and *P. neriifolia* but high for *P. lacticolor*. It would appear that Kruger and Lambs' hypothesis (1979) that the minimum age for population replacement is when at least 50% of the plant in the population have flowered for more than three seasons may be an overestimate for *P. neriifolia* and *L. xanthoconus*, but it will be wiser to apply their rule of thumb as this will ensure that adequate seed banks are present.

2.7 Conclusions

This study has confirmed the common observation that mortality rates of seed-regenerating Proteaceae are higher in old stands (20+ years) and is the first to demonstrate that the increase is statistically significant. The different species matured at much the same age (4-5 years) and, for *Protea lacticolor,* even across a range of soil moisture conditions where plants on the wettest sites grew faster than those on dryer sites (Kruger 1987). Seed bank accumulation rates appear to be low compared with reports for other species (e.g. Bond 1985) but this may be due to sampling at a relatively young age of 10 years. *Protea lacticolor* accumulated the most seeds on the driest site and least on the wettest site, although plants on the wettest site were substantially taller than those on the driest sites. Net seed banks were marginal for population replacement, given the best available estimates of seedlings per seed, but populations appear to have been stable at about their current densities over three fire cycles. Seed losses to insects were low but baboon damage could result in the loss of 20% of the seed crop. Overall, all three species appear able to maintain their populations although a lower fire frequency would provide a greater insurance against poor conditions for recruitment such as a spring fire or an unusually long and dry first summer.

Chapter 3: Canopy-stored seed banks of two shrubs (*Protea repens* and *Protea neriifolia*, Proteaceae), Cape Province, South Africa: effects of stand density and age

3.1 Abstract

Seed-bearing inflorescences of eight, twelve and twenty-eight year old *Protea neriifolia* R.Br. and twenty-eight year old *P. repens* (L.) L. shrubs were harvested at five sites in the Jonkershoek Valley, Western Cape Province, South Africa. The inflorescences were divided into three age classes: (i) most recent with mature seeds, (ii) the previous seasons and (iii) all the remaining seed-bearing inflorescences. The proportion of *P. neriifolia* plants in flower increased annually in nine and twelve year old populations. In twenty-eight year old populations of *P. neriifolia* and *P. repens* the proportion of plants in flower decreased in successive years. The number of seed-bearing inflorescences increased rapidly with age and size in *P. neriifolia*. The number of seed-bearing inflorescences of twenty-eight year old *P. repens* plants was markedly lower than that of co-occurring *P. neriifolia* plants primarily because extensive insect damage to *P. repens* inflorescence causes them to open and shed their seeds. There was a significant decline in the number of full seeds from inflorescence age-class 1 to 2 in both species. *Protea repens* had a high number of full seeds per inflorescence in the youngest age class, but few full seeds in older inflorescences because of seed predation by insects. *Protea neriifolia* had fewer full seeds per inflorescence but there was a slow rate of decline in the number of seeds per inflorescence. Most of the full seeds of the twenty-eight year old *P. neriifolia* shrubs were in inflorescences from the oldest age class. Although the number of seeds per shrub of both species declined with increasing stand density, the number of seeds per square metre increased, more than compensating for the decline in unit output. The density related decline in seed banks per plant was less marked for *P. repens* than for *P. neriifolia*, but *P. repens* had fewer seed-bearing inflorescences per shrub at equivalent densities. *Protea neriifolia* and *P. repens* are ecologically and morphologically similar but differ in inflorescence production and seed-bank dynamics and in their responses to stand density. Both species would exhibit a marked seasonal cycle in the number of seeds in the seed bank when young. This cycle would be damped out by the accumulation of seeds in the persistent inflorescences of older *P. neriifolia* plants, but the reserves of *P repens* would continue to fluctuate because of the high seed-predation rates by insects in this species. Thus fires at different intervals and in different seasons could influence the relative reproductive success of these two species.

3.2 Introduction

Tall seed-regenerating shrubs of the family Proteaceae are an important component of the fire-prone sclerophyllous shrublands of the southern and south-western Cape, South Africa (Taylor 1978) and of parts of western and south-eastern Australia (Lamont *et al.* 1985). Many shrubs in the genera *Protea*, *Leucadendron* and *Aulax* (Cape) and *Banksia* and *Hakea* (Australia) store their seeds in persistent inflorescences or infructescences (Lamont, Collins & Cowling 1985). A number of studies have quantified the seed banks of Cape Proteaceae (Lombaard 1971; Bond 1985; Mustart *et al.* 1994; chapter 1) and examined the effects of stand density on seed banks (Esler & Cowling 1990; Maze & Bond 1996). Esler and Cowling (1990) sampled three stands (one on a different site) and found that seeds per plant of *Protea lepidocarpodendron* declined with increasing stand density but seeds per unit area increased. Maze and Bond (1996)found that that seeds per unit area also declined at high stand densities for *P. neriifolia* and *P. repens*. Information on seed bank dynamics and age-specific fecundity is available for Australian Proteaceae (e.g. Cowling, Lamont & Pierce 1987; Bradstock & O'Connel 1988) and this will be discussed later.

Protea neriifolia R.Br. and *Protea repens* (L.) L. are tall, evergreen shrubs with a similar form and appearance. Both species have a wide distribution in the fynbos biome with the more widespread *P. repens* ranging into dryer areas than *P. neriifolia* which occurs mainly in the wetter southern mountain ranges (Rourke 1980). *Protea neriifolia* flowers from April to July with a peak in June (Rourke 1980). In the Western Cape *P. repens* flowers from March to October with a peak during April and May (Jordaan 1949). Seeds of both species mature about seven to eight months after flowering (Jordaan 1949; Van Staden 1978). Both species are killed by fires and regeneration depends entirely on seeds accumulated in the persistent woody inflorescences. Seedling recruitment is generally confined to the first winter after a fire so that populations are even-aged (Kruger & Bigalke 1984). Flowering begins at three to five years of age and senescence at 30 to 50 years of age (Bond 1980, Kruger & Bigalke 1984). In the study area *P. neriifolia* is generally dominant on deeper soils derived from granites and *P. repens* on shallower rocky soils derived from a mixture of granite-derived soils and sandstone talus. They also, however, occur in mixed or single species stands on either soil type (McDonald 1988).

This study examined the dynamics of the seed banks of *P. neriifolia* and *P. repens* and addressed the following questions:

(i) How do plant size, age (only *P. neriifolia*) and stand density influence the production of inflorescences, and thus seeds, and how does this differ between these two species?

(ii) What is the relative composition of the seed banks in terms of current versus older inflorescences and how does this vary between these species and with increasing age in *P. neriifolia*?

I have used inflorescences here to mean seed-bearing inflorescences, those that had already released their seeds were excluded.

3.3 Materials and methods

3.3.1 *Study sites*

The study sites were situated in the Jonkershoek Valley (33°57'S, 18°55'E), South Africa. The climate of the area is characterized by cool wet winters and a warm dry summer (mean daily temperature below 22°C for the warmest month). The mean annual rainfall at the sample sites is about 1700-1900 mm. The soils are loams derived from Cape granites or quartzitic sandstones of the overlying Peninsula formation or mixtures of the two (Fry 1987). Granite-derived soils are finer textured and have significantly higher levels of organic matter and nutrients than quartzite-derived soils, which are also more rocky (Fry 1987). The entire study area was burnt in 1927, in December 1942 and in February 1958. Sites 3, 4 and 5 (Table 3.1) were located in the area last burnt in 1958. Site 2 was located in an area which was burnt in November 1973 (Van Wilgen & McDonald 1992) and Site 1 in an area burnt in August 1977. Stand ages are calculated using June of the year after the fire as the seed germination date (Table 3.1). Preliminary analyses showed that the twenty-seven and twenty-eight year old stands did not differ significantly in seed bank composition so they are treated as twenty-eight years old to simplify discussion.

The vegetation on the study sites was a proteoid shrubland (Van Wilgen 1981, McDonald 1988) which varied in height from 1.2 m at 8 years to 3.5 m at 28 years of age. At sites 1, 2 and 4 (Table 3.1) the overstorey was open but at sites 3 and 5 there was a closed overstorey. At site 4 there were a few clumps of *Widdringtonia nodiflora* (L.)Powrie (Cupressaceae), a multi-stemmed resprouting tree species up to 4 m tall, interspersed between the proteas.

3.3.2 *Seed bank sampling*

The sites were selected to obtain data on the seed banks of *Protea neriifolia* populations of eight, twelve and twenty-eight years of age within a relatively homogeneous area, and also to obtain data on the seed banks of *P. neriifolia* and *P. repens* in similar sites at twenty-eight years of age. A

sample transect was laid out at each site (Table 3.1). All the inflorescences of each shrub rooted within the sample transect (Table 3.1) were removed and divided into three age classes as follows:

Class 1: most recent inflorescences with mature seeds (1985 or 1986 flowering season). Inflorescences from the 1986 flowering season were not collected at site 1 because the seeds were not yet mature.

Class 2: previous crop of inflorescences (1984 or 1985 flowering season)

Class 3: All previous inflorescences bearing seeds. Most of these inflorescences were three or four years old but some retain seeds for up to seven years. At site one, 1983 was the first flowering season except for one shrub which bore a single inflorescence in 1982.

Inflorescences were separated into these age classes on the basis of their position on the branches of the shrub, the colour and weathering of the involucral bracts and the age of the leaves on the branch or shoot, if present. The number of inflorescences of each of the 19 *P. neriifolia* shrubs at site 2 was counted. The inflorescences of these plants were not harvested because the site formed part of a long-term study of the population dynamics of *P. neriifolia*. The number of seeds per plant was estimated from the number of seed per inflorescence of a sample (wandering quarter technique, Catana 1963) of 20 shrubs adjacent to site 2.

Closed inflorescences were opened by drying them in the open air or in a forced draught oven at 30-40 °C. Seeds of *P. neriifolia* were classified as full on the basis of firmness and colour (Horn 1962). The hard woody seeds of *P. repens* were cut open and classified as full if they had a firm, white embryo. The stem diameter below the first branch and number of inflorescences and seeds per inflorescence age-class of each shrub was recorded.

The mean number of inflorescences and seeds per shrub was calculated for shrubs with inflorescences in a given age-class and the sample sizes are given in the tables. Seed yield per inflorescence was calculated by dividing the number of seed by the number of inflorescences in each age class of each shrub. Seed densities were calculated from the total number of seeds (per age class) collected (sites 1, 3, 4 and 5), or estimated (site 2), divided by the sample area in square metres.

Table 3.1: Details of the environments, stand age and stand density, and sample sizes at five study sites in the Jonkershoek Valley.

Site number	Species present	Stand age[1] (years)	Aspect	Altitude (m)	Slope (deg)	Soil parent material	Size of sample transect	Sampling date	Stand density (plants per ha)
1	*P. neriifolia*	8	NE	500	17	Granite	10 x 35 m	August 1986	2114
2	*P. neriifolia*	12	E	480	7	Sandstone talus/granite	50 x 50 m	February 1987	76
3	*P. neriifolia* and *P. repens*	27	NE	420	0-2	Granite	10 x 40 m	February 1986	4400
4	*P. neriifolia* and *P. repens*	28	N	500	15	Sandstone talus/granite	10 x 30 m	January 1987	1376
5	*P. repens*	28	N	460	35	Sandstone	10 x 10 m	December 1986	19200

1: Stand age was calculated using June of the year after the fire as the germination date.

3.3.4 *Statistical analyses*

The effects of stand density and plant age on the slope and intercept of the regression of the number of seed-bearing inflorescences on stem diameter were determined by means of a multiple linear regression analysis (GLM procedure, SAS 1985). As the partitioning of variance in this analysis is influenced by the sequence of entry of the variables into the regression model, an additional analysis in which the variables are selected independently was also used. The best subsets of independent variables were selected using a stepwise multiple linear regression procedure and Mallow's C(P) statistic (RSQUARE procedure, SAS 1985). Hoerl's model $y = ax^bc^x$ (in linearised form: log y = loga +blog x+xlog c) was used for the regression of the number of seed bearing inflorescences (y) on stem diameter below the first branch (x) because it gave a better fit (higher R^2) than power and linear models. Natural logarithms ($\log_e$) were used throughout. The significance of the differences between age classes in the number of seeds per inflorescence was determined using an Analysis of Variance with a Tukey's studentised test (GLM procedure, SAS 1985). The coefficient of variation was used as a measure of the skewness of the size distribution in the sampled plant populations (Bendel *et al.* 1989).

3.4 Results

The multiple linear regression analysis showed that the number of inflorescences of *P. neriifolia* was significantly related to stem diameter, or log stem diameter, and stand age (Table 3.2) but the slope and elevation of the relationship between stem diameter and the number of inflorescences did not differ significantly between plants of different ages (diameter x age, $P>0.05$ - Table 3.2). The relationship between stem diameter and the number of inflorescences of twenty-eight year old *P. neriifolia* was significantly influenced by the different densities of the stands at sites 3 & 4 (Tables 3.1 and 3.2). These results were confirmed by the inclusion of both stem diameter and stand density in the best sub-set of variables for predicting the number of inflorescences (Table 3.3). On the basis of this analysis separate regression models were fitted to the data for *P. neriifolia* for the following sets of sites: (a) site 1, (b) combined twelve year old samples (site 2), and (c) site 3 and site 4 separately (Table 3.4). A similar analysis for *P. repens* showed that the relationship between stem diameter and the number of inflorescences only differed significantly between sites 3 and 4 on the one hand and site 5 on the other (Table 3.2). Again this was confirmed in the selection of the best subset of variables for *P. repens* (Table 3.3) and separate models were fitted to data for (a) sites 3 and 4 combined and (b) site 5 (Table 3.4).

3.4.1 *Inflorescence production*

3.4.1.1 Influence of plant size on inflorescence production

There was a non-linear relationship between plant size (using stem diameter as an index of size) and the total number of inflorescences (Fig 3.1). In the case of *P. neriifolia* both diameter and log stem diameter were chosen as independent (explanatory) variables (Table 3.3). For *P. repens* only stem diameter was selected (Table 3.3) but log stem diameter was included in the site models (Table 3.4) as it improved the fit of the regression. For example the coefficient of determination for the regression for site 5 increased from 0.51 to 0.73 with the inclusion of log stem diameter. The relationship between plant size and the total number of inflorescences differs between the two species (Fig 3.1, Table 3.4). At site 3 *P. neriifolia* had more inflorescences than *P. repens* at any given stem diameter. At site 4 it had an equivalent number of inflorescences on smaller plants but substantially more on those with a stem diameter greater than 70-80 mm (Fig 3.1). *P. repens* had a maximum of 55 and 47 seed bearing inflorescences at sites 3 and 4 respectively compared with corresponding values of 158 and 260 inflorescences in *P. neriifolia*.

The mean stem diameter (below first branch) of mature twelve year old *P. neriifolia* plants (plot sample 33.1 mm, S.E. 4.2, n=14) was significantly smaller than that of eight year old plants (54.8 mm, S.E. 8.4, n=67) ($P<0.05$, Student-Newman-Keuls test, GLM procedure SAS 1985). Stem diameter is strongly correlated with the number of inflorescences (Table 3.4) so the relatively low mean inflorescence production (Table 3.5) was largely due to the smaller size of the twelve year old plants.

3.4.1.2 Influence of plant age on inflorescence production

There is an increase in the total number of seed bearing inflorescences with increasing age (Table 3.3, Fig 3.1) with some twenty-eight year old *P. neriifolia* plants carrying about 250 inflorescences (Fig 3.2). One shrub at site one had flowered in 1982, at four years of age. In 1983, twenty eight (35%) flowered and in 1985 seventy seven percent. At site three, however, the proportion of the population remained relatively constant at about 46% from 1984 to 1986 (Table 3.5). On the other hand, twelve year old plants with a stem diameter greater than 50 mm bore more inflorescences than equivalent eight year old plants (Fig 3.1) because they had accumulated more class 3 inflorescences and bore more class 1 inflorescences (Table 3.6).

Table 3.2. A multiple linear regression analysis of the effects of plant size, age and stand density on the relationship between the total number of seed-bearing inflorescences (dependent) and the stem diameter of the shrub below the first branch (independent variable) in two *Protea* species. An 'x' indicates a test of the interaction between two factors. The sum of squares for each parameter or interaction is the additional sum of squares explained by the model due to the addition of that parameter to the ones above.

Species	Parameter	Sum of squares	F-value
P. neriifolia	Diameter	48.25	344.56**
	Log diameter (Log di)	2.11	15.05**
	Age	2.18	15.59**
	Diameter x age	0.01	0.05
	Diameter x (density:site 3 versus 4)	1.93	13.81**
	Log di x age	3.69	3.69
	Log di x (plot vs random: 12-yr old)	0.05	0.38
	Log di x (density: site 3 versus 4)	1.19	8.51**
P. repens	Diameter	15.76	157.28**
	Log diameter (log di)	0.05	0.49
	Density	3.66	36.57**
	Diameter x (density: site 3 vs 4)	0.02	0.20
	Diameter x (density: site 3 & 4 vs 5)	0.16	1.62
	Log di x (density: site 3 vs 4)	0.12	1.21
	Log di x (density: site 3 & 4 vs 5)	1.83	18.22**

**: $P<0.01$

Table 3.3. The optimal subsets of variables selected for a multiple linear regression model of the total number of inflorescences on stem diameter below the first branch in two *Protea* species. The optimal subsets were identified as those giving the highest R^2 and a Mallows C(P) statistic less than the minimum number of variables in the subset plus the intercept.

Species	Parameter	Sum of squares	F-value	Mallow's C(P) statistic
P. neriifolia	Diameter	0.74	5.30*	5.34
	Log diameter (Log di)	3.17	22.67**	
	Log di x (density: site 3 vs 4)	1.93	13.86**	
	Diameter x (density: site 3 vs 4)	0.99	7.06**	
P. repens	Diameter	12.47	127.54**	1.34
	Diameter x (density: 3 & 4 vs 5)	2.42	24.72**	
	Log di x (density: 3 & 4 vs 5)	3.45	35.28**	

*: P<0.05, **: P<0.01

Table 3.4. Regression models for the relationship between stem diameter (mm) below the first branch and the total number of seed bearing inflorescences on shrubs of *P. neriifolia* and *P. repens*. Details of the sites and sample populations are given in Table 3.1. The linear transformation of Hoerl's model $y = ax^bc^x$ was used throughout because it gave the best fit (R^2).

Site	Species	Sample size	Intercept $\log_e(a)$	Exponent (b)	Constant $\log_e(c)$	R^2	F value
1	P. neriifolia	67	-1.9601	-0.0246	0.7362	0.54	37.12**
2	P. neriifolia	37	-0.8460	0.0849	-0.5736	0.88	39.39**
3	P. neriifolia	115	-4.7201	0.0117	1.5210	0.57	75.95**
	P repens#	46	-3.5892	-0.0034	1.4193	0.48	21.39**
4	P neriifolia	18	-4.3205	0.0014	1.8450	0.51	6.91**
5	P repens	68	5.6315	0.0805	-2.2655	0.66	63.93**

#: The same model was fitted to the *P. repens* data for both sites 3 and 4 because the preliminary analyses (Table 3.4) revealed that there were no significant differences between the regression relationships for these sites.
**: $P < 0.01$.

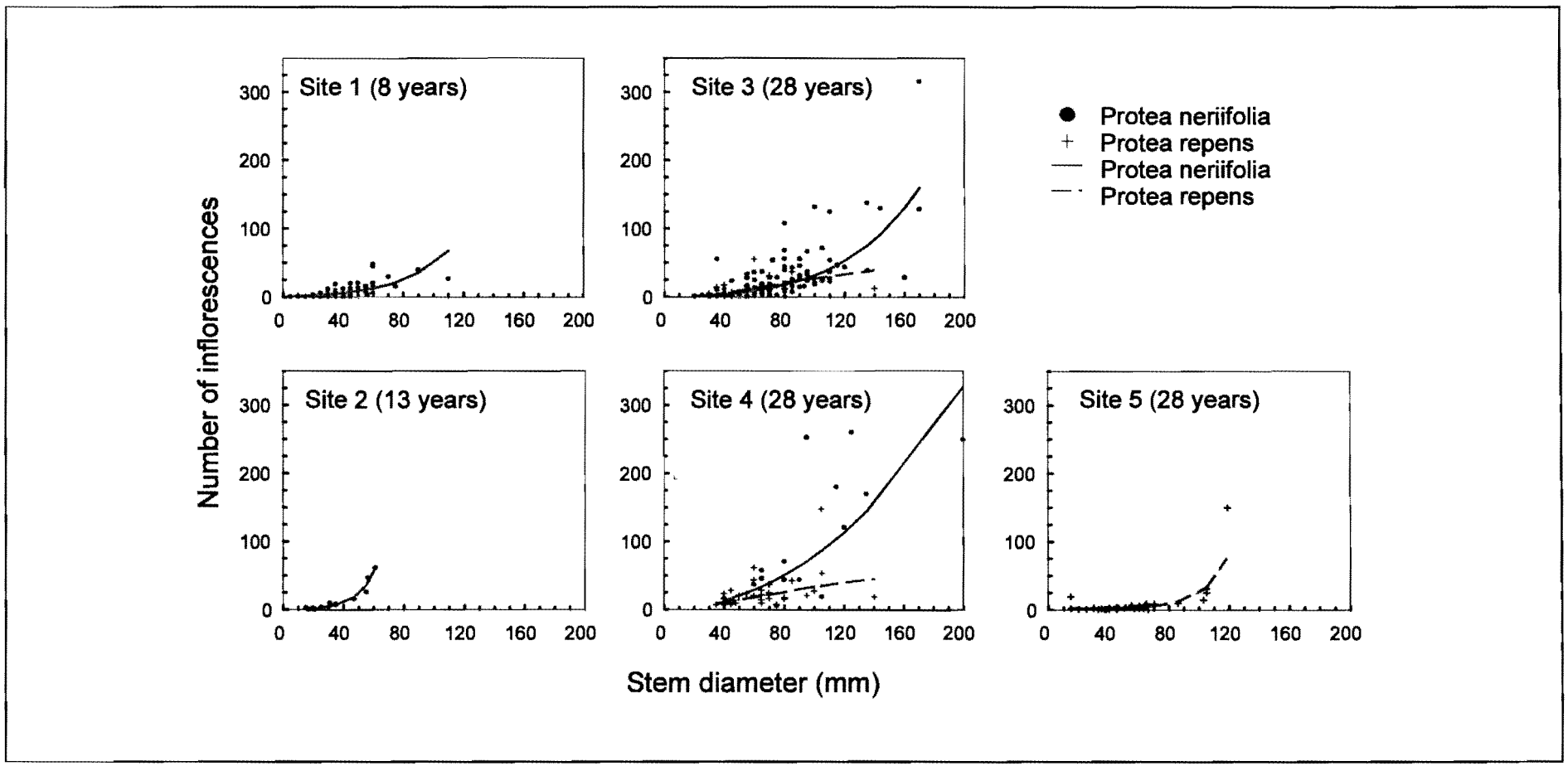

Figure 3.1 The relationship between stem diameter (mm) below the first branch and the number of seed bearing inflorescences at five sample sites (Table 3.1). The raw data have been omitted to facilitate comparisons of the differences between sites and species (Table 3.6). (———) = *P. neriifolia* and (------) = *P. repens*. The regressions models used for the curves are given in Table 3.4.

Table 3.5: Statistics of each of the five sample populations and the fluctuations in the number of *Protea neriifolia* and *P. repens* plants that flowered in each year. The number "with no flowers" was the number of live plants in the population which had no seed bearing inflorescences at all. The number of plants with inflorescences in a given age class was used to determine the number of plants in flower in the corresponding year. The age class is given in parentheses.

Site No.	Species	Number of plants						
		Total		With no	Which flowered in each year			
		live	dead+	flowers	1983	1984	1985	1986
1	neriifolia	74	1	7	28(3)	50(2)	57(1)	-
2	neriifolia	19	0	5	-	11(3)	11(2)	10(1)
3	neriifolia	140	8	25	102(3)*	100(2)	69(1)	63#
3	repens	33	2	12	19(3)*	15(2)	9(1)	-
4	neriifolia	20	0	2	-	16(3)*	16(2)	16(1)
4	repens	34	2	1	-	22(3)*	25(2)	10(1)
5	repens	192	48	126	-	25(3)*	49(2)	28(1)

+: dead adult plants only
*: Includes all plants with seed-bearing inflorescences from previous flowering seasons
#: Determined during a second census of the population in March 1987

A large proportion of the twenty-eight year old plants of both species have fewer than 25 inflorescences, including some of the medium sized plants (Fig 3.3). At site 3 only sixty-nine *P. neriifolia* plants flowered in 1985 compared with 100 in 1984 (Table 3.2). The same trends are evident in the samples from twenty-eight year old *P. neriifolia* plants classified as alive at site 3 in August 1986 which had died or were dying by March 1987. These dead or dying plants yielded only 9% of the inflorescences produced in 1985 and 6% of the seeds, a significantly lower proportion than the survivors (Chi-square value 58.2 $P < 0.001$), evidence of a steep drop off in reproductive output shortly before death.

3.4.1.3 Influence of stand density on inflorescence production

There were significant differences in the relationship between stem diameter and total seed bearing inflorescences in stands at different densities - site 3 versus 4 for *P. neriifolia* and sites 3 and 4 versus site 5 for *P. repens* (Table 3.2, Figs 3.1 and 3.2). *P. neriifolia* plants at site 3 (4 400 per ha) had fewer inflorescences at a given stem diameter than at site 4 (1 350 per ha). The number of inflorescences of *P. repens* plants at sites 3 and 4 was similar (Table 3.6) but there were markedly less inflorescences per *P. repens* shrub at site 5 (19 200 per ha). The highest annual inflorescence production of *P. neriifolia* was

in the open stand at site 4 (Table 3.6). There was relatively little decline in the mean number of inflorescences per non-barren *P. repens* shrub with increasing density.

The proportion of live plants with no seed-bearing inflorescences increased with increasing stand density from 10% to 18% of *P. neriifolia* plants at sites 4 and 3 respectively (Figs 3.2 and 3.3). The corresponding values for *P. repens* were 3 and 36%, but 66% of the plants at site 5 had no inflorescences (Figs 3.2 and 3.3). The proportion of dead plants increased from zero (site 4) to 6% (site 3) in *P. neriifolia* and from 6% (sites 3 and 4) to 25% (site 5) in *P. repens* (Table 3.5). These trends suggest that competition in the more dense stand had reduced inflorescence production (Fig 3.2).

3.4.2 *Seeds per plant*

The number of seeds in class 3 inflorescences increased from about 0.3 times the current crop (class 1) of in eight-year old to about 1.7 times the current crop in twenty-eight year old *P. neriifolia* old plants (Table 3.6). At twenty-eight years of age a large proportion of seeds of *P. neriifolia* were in age class 3 (47% site 3, 35% site 4; i.e. from inflorescences ≥3 years old) while most *P. repens* seeds were in age class 1 (80% site 3, 66% site 4) except at site 5 (40%). In both species there was a marked decline in the number of seeds per plant with increasing stand density, particularly *P. repens* at site 5 (Table 3.6). Seed reserves of the twelve year old *P. neriifolia* plants were generally lower and declined more rapidly than in the other populations (Table seeds per 3.6).class 1 inflorescence than *P. repens*, but the rate of decline was much higher in the latter species, mainly due to seed predation by the larvae of insects (Coetzee & Giliomee 1987).

3.4.3 *Seeds per inflorescence*

Stand density appears to have had little effect on the number of seeds per inflorescence in *P. neriifolia* and *P. repens* at sites 3 and 4, but there was a significant decline in the number of full seeds per inflorescence with increasing inflorescence age in both species (Table 3.6). *P. neriifolia* generally had fewer seed per class 1 inflorescence than *P. repens*, but the rate of decline was much higher in the latter species, mainly due to seed predation by the larvae of insects (Coetzee and Giliomee 1987). Stand density appears to have had little effect on the number of seeds per inflorescence in *P. neriifolia* and *P. repens* at sites 3 and 4, but there was a drop in seed yield per inflorescence in the dense *P. repens* stand at site 5.

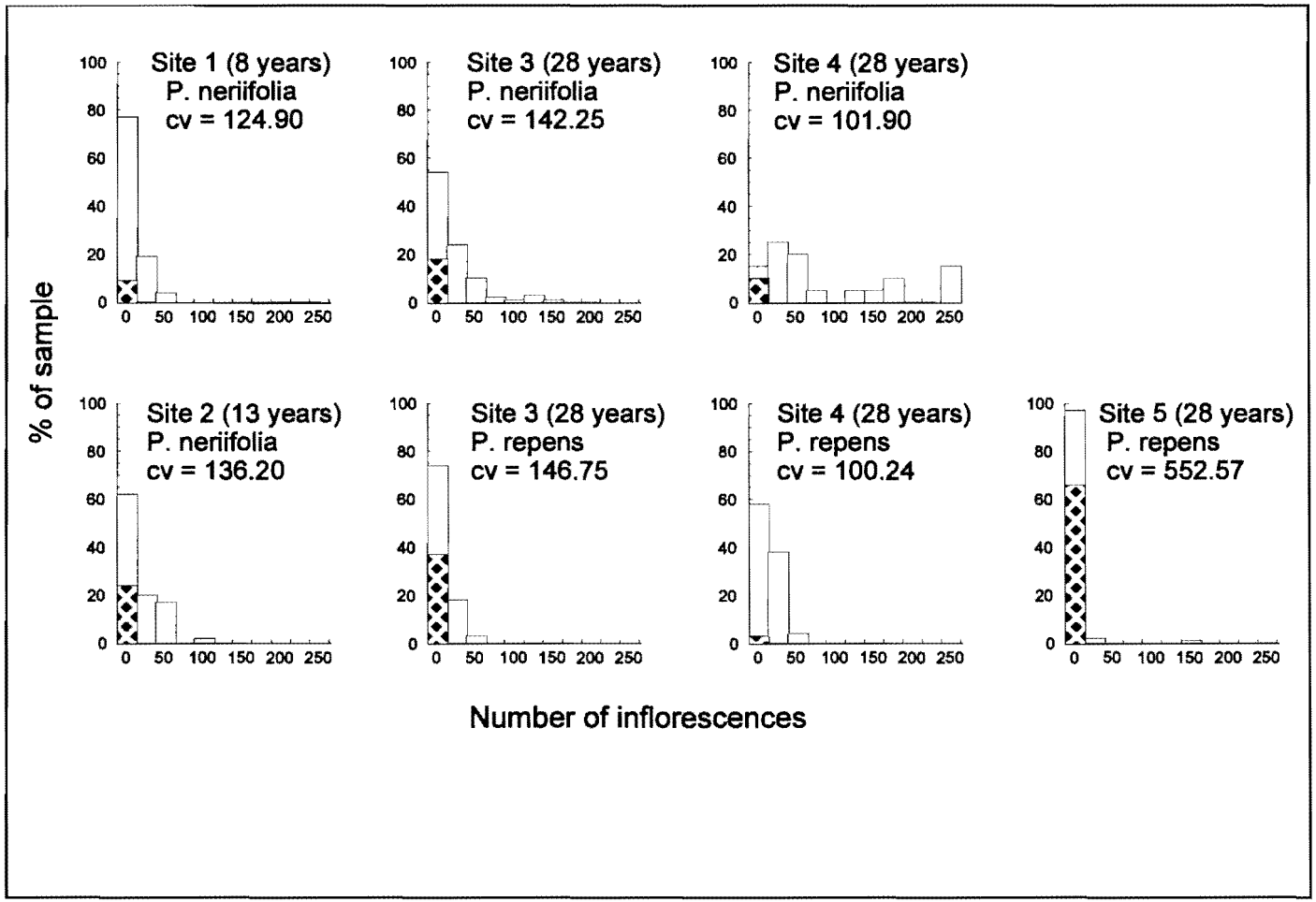

FIG. 3.2. Frequency distributions of the number of inflorescences per plant at five sample sites (Table 3.1). The proportion of the sample plants with no inflorescences is given by the shaded bars. CV = Coefficient of variation (percent). Class intervals in units of 25 (e.g. 0-24.99, 25-49.99...).

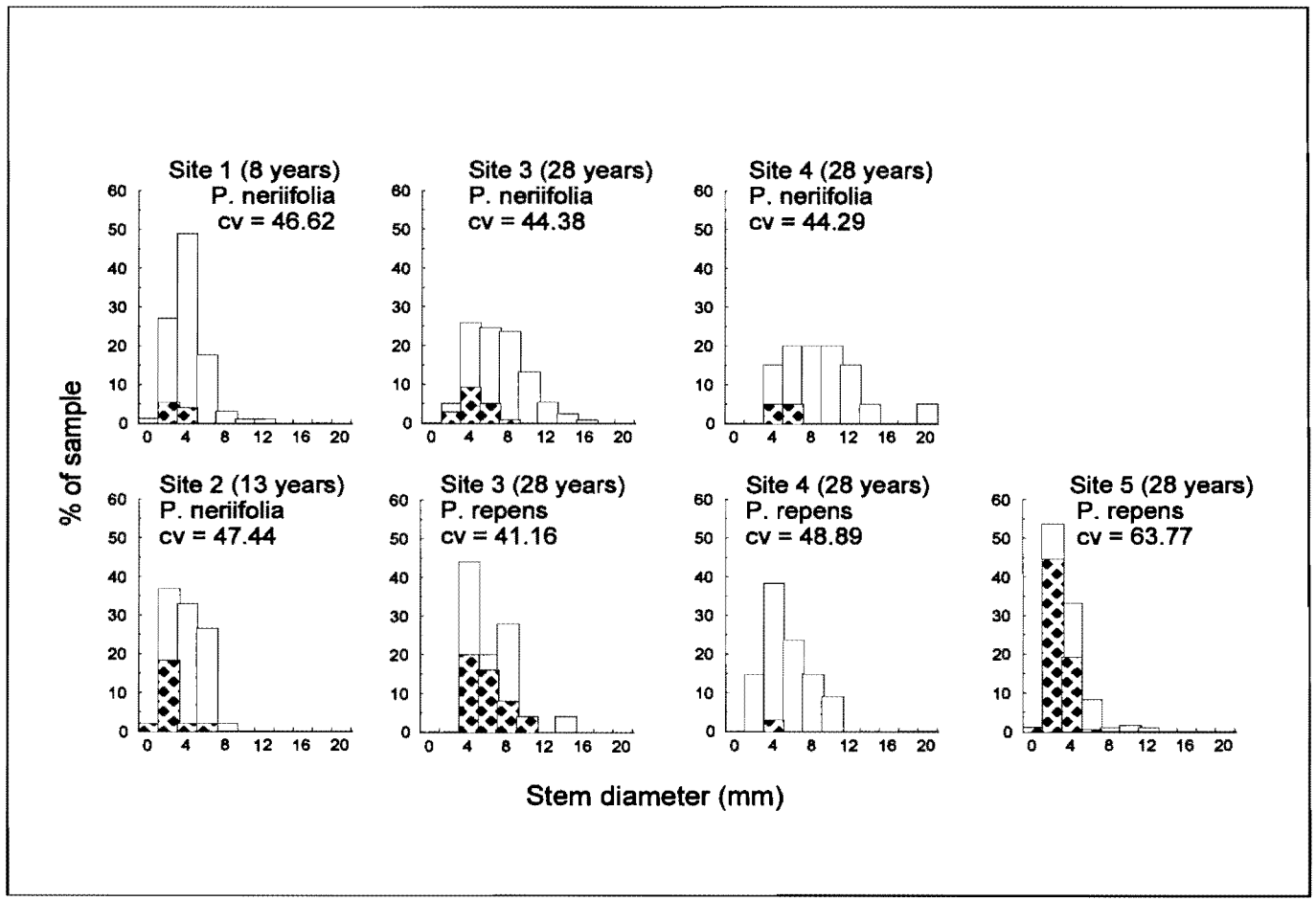

FIG. 3.3. Frequency distributions of the stem diameter of the plants at five sample sites (Table 3.1). Separate histograms are given for *P. neriifolia* and *P. repens* at sites where they co-occurred. The percentage of the plants with no inflorescences in each diameter class is given by the shaded bars. CV = coefficient of variation (percent). Class intervals 20 mm.

Table 3.6: Data on the seed banks of *Protea neriifolia* and *P. repens* from five sites (see Table 3.1 for more details of the sites). The values in the table were calculated only for shrubs bearing inflorescences of that age class (the corresponding sample sizes are given in Table 3.5). The standard error of the mean is given in parentheses. Values for seed yield in classes which have the same symbol are not significantly different (Tukey's studentised test, GLM procedure, SAS 1985, $P > 0.05$).

Parameter	SITE						
	1	2	3	3	4	4	5
Stand age	8	12	27	27	28	28	28
Stand density (/ha)	2114	76	4400	4400	1376	1376	19200
Species	nerii	nerii	nerii	repens	nerii	repens	repens
Number of inflorescences per plant:							
Age class 1	3.8(0.4)	7.5(2.5)	6.3(1.3)	3.7(1.0)	19.6(4.1)	2.8(0.4)	2.0(0.4)
Age class 2	5.9(0.9)	4.3(1.2)	9.6(1.1)	5.9(1.1)	17.9(3.8)	5.5(1.9)	4.1(1.5)
Age class 3	3.2(0.6)	6.4(2.7)	17.0(2.4)	9.2(2.3)	72.4(16.1)	9.6(1.6)	5.5(2.9)
Number of full seeds per plant:							
Age class 1	34.5(5.9)	33.9(12.1)	18.1(4.2)	45.0(22.9)	47.4(18.0)	33.2(8.5)	6.4(1.4)
Age class 2	33.0(7.6)	10.7(3.6)	16.9(3.2)	10.4(2.9)	32.9(17.7)	13.2(5.4)	5.1(3.7)
Age class 3	11.3(13.8)	8.2(2.6)	31.6(6.6)	1.0(0.5)	43.9(13.0)	3.6(1.5)	4.7(4.0)
Number of full seeds per inflorescence#:							
Age class 1	9.6(1.8)a	2.9(0.8)a	2.9(0.6)a	12.9(3.0)a	2.6(0.7)a	16.9(4.2)a	4.1(1.0)a
Age class 2	4.7(0.7)b	0.8(0.2)b	1.9(0.3)b	3.4(1.3)b	1.6(0.5)ab	5.0(2.4)b	0.8(0.4)b
Age class 3	2.5(0.7)b	0.5(0.2)b	1.6(0.3)b	0.1(0.1)b	0.6(0.2)b	0.3(0.1)b	0.6(0.4)b
Number of full seeds per square metre+:							
	11.3	0.12*	15.4	1.5	5.0	1.9	5.5

#: Calculated as number of seed per shrub divided by number of inflorescences per shrub.
+: Seeds per shrub x number of shrubs per m^2.
*: Number of seed per inflorescence estimated from separate sample (see methods).

3.4.4 *Seed density*

The net result of the trends described above is given by the seed density for the stand (Table 3.6). The eight year old stand (site 1) had more seeds per unit area than a twenty-eight year old stand (site 3), despite the lower density of the stand (Table 3.3). There was an increase in the seed density with

increasing stand density in the twenty-eight year old stands despite the decline in the seed yield and number of plants in flower of both species (Tables 3.5 and 3.6 and Fig 3.2).

3.5 Discussion

This study has followed the approach of sampling different sites of different post-fire ages and treating them as equivalent to a series of observations at the same site at different times. It is an approach that has been used in other studies (Specht, Rayson and Jackman 1958, Gill & McMahon 1986). The environments at the sites used in this study were not identical (Table 3.1). For example the sources of the soils differ, particularly between sites 2 and 5 and the rest (Table 3.1). As argued earlier, the importance of nutrient-poor sandstone derived soils at site 2 (Table 3.1, Fry 1987) may be the primary cause of the relatively low seed yield of twelve year old shrubs compared with eight year old shrubs at site 1 (Table 3.6, Figs 3.2 and 3.3). Site 5 is situated on a more exposed well drained slope than sites 3 and 4 so the shrubs could be more moisture stressed in summer and consequently smaller and less fecund. Studies of *P. repens* near site 5 and on the same slope have shown, however, that it experiences little moisture stress during summer (Richardson & Kruger 1990). Nervertheless there could be some confounding of patterns due to age, soil and stand density and this must be borne in mind.

Does the influence of stand density differ from that of moisture stress in ways that would support the argument that these sites can be compared? Moisture stress would be expected to influence all individuals so that the entire population should be generally smaller in size (Harper 1977). In contrast, inter-plant competition in even-aged stands generally results in the formation of a skewed size distribution with most plants falling in the smaller size classes (Harper 1977, Weiner & Solbrig 1984). The skewness of the diameter distribution also tends to increase with plant age and increasing stand density (Harper 1977, Mack & Harper 1977). While plant size differs between sites 3, 4 and 5, the most marked differences are in the increasing skewness (higher Coefficient of Variation) of the size distribution with increasing stand density (Table 3.1, Fig 3.3). This supports the argument that the influence of stand density in this study is greater than the influence of differences between sites, but does not entirely negate the influence of site factors.

The fecundity of the plants is even more skewed than the size distribution at high stand densities (Fig 3.2), so that the composition of the next generation will be determined largely by the reproductive output of a few individuals. The evolutionary consequences of this skewed fecundity are significant, especially in terms of gene-flow and the size of the effective gene pool (Wilson & Levin 1986). The

most extreme example is the dense *Protea repens* population at site 5 where only 66 of the plants had produced inflorescences and only 15 (7.8%) had accumulated any seeds. Thus less than 10% of the potential maternal gene pool would contribute to the next generation. In addition, one plant had 294 seeds, 54% of the total, so that its maternal genes would dominate the gene pool of the seedlings after the next fire.

The two *Protea* species also appear to differ in their response to stand density: *P. neriifolia* produced fewer inflorescences per shrub with increasing density while individual *P. repens* plants were less likely flower at all as stand density increased (Fig 3.2, Tables 3.5 and 3.6). The same trend in *P. repens* was also found by Maze and Bond (1996) suggesting that it may be a general pattern and possibly related to this species architecture and inflorescence growth patterns (Bond *et al.* 1995; see also Le Maitre & Midgley 1991).

A number of studies have provided data on the dynamics of canopy seed banks of serotinous Cape Proteaceae and a few have examined the effects of density or age. The seed banks of *P. repens* and *P. neriifolia* found in this study fall within the range of those reported in other studies of *Protea* species (Table 3.7) although some species, eg. *P. burchellii* and *P. lepidocarpodendron* may have considerably larger seed banks (Table 3.7). *Protea repens* populations occur within 50 m of site 1 and the inflorescence production of shrubs on unfertilized control plots was recorded by Lamb & Klaussner (1988) during 1983 and 1984. Forty-four plants (25.9% of the total) flowered in 1983 and produced 1.64 (S.E.=0.15) inflorescences and 45 plants produced 2.84 (S.E.=0.34) seed-bearing inflorescences in 1984. Both the percentage of plants in flower and the inflorescence production are lower than those of *P. neriifolia* of the same age and in the same years (Tables 3.5 & 3.6). Stand density was also found to have a marked effect on the number of seeds per plant in *P. lepidocarpodendron* (Table 3.7), but seed density (number per unit area) increased despite the decline in seeds (and inflorescences) per plant (Esler & Cowling 1990), as in this study (Table 3.6). This is contrary to the decline in inflorescence numbers per unit area found by Maze & Bond (1996) for a similar range of stand density. Maze and Bond (1996) sampled a wide range of stand densities matched for site and age so their conclusion that that seeds per unit area also declined at high stand densities for *P. neriifolia* and *P. repens* is the most strongly supported and also accords with the findings of studies of seed regeneration success (e.g. Bond *et al.* 1994; see also Bond *et al.* 1995).

Seed banks of some Australian *Banksia* species can be 3-10 times or more greater than those of *Protea* species but most are quite similar (Table 3.7) and low by comparison with seed banks of species with soil-stored seeds. Different studies have shown that there is a wide range in the number

of seeds in the seed banks of the same species in both *Protea* (Table 3.7) and *Banksia*, regardless of stand age or other factors. For example the regression model of Bradstock & O'Connel (1988) predicts viable seed banks of 10.6, 16.5 and 26.0 seeds per *B. ericifolia* plant at 8, 12 and 28 years of age respectively. This is far less than the 1368 seeds per plant given by Carpenter & Recher (1979, Table 3.7). These seed banks are very small compared with many species with soil-stored seeds (see Le Maitre & Midgley 1992). Serotinous Proteaceae must, therefore, be very effective at converting seeds into seedlings if they are to maintain viable populations. A first estimate was provided by Le Maitre & Midgley (1992) who collated data suggesting that serotinous Proteaceae have seed : seedling ratios of about 0.05-0.44 compared with 0.001-0.01 for fynbos and chaparral species with soil-stored seeds. Maze & Bond (1996) give estimates of 0.46-0.57, again one to two orders of magnitude more efficient than species with soil-stored seeds.

Table 3.7. Comparative data on the canopy seed banks seed regenerating Proteaceae: *Protea* (Cape) and *Banksia* (Australia) Proteaceae.

Species	Stand age (years)	Plants per ha	Viable seeds per shrub: Current crop	Viable seeds per shrub: Previous crop	Viable seeds per shrub: Total	Source
P. aurea	17	-	60.0	35.3	109.7	Bond 1985
P. burchellii	11	-	-	-	156.5	Lombaard 1971
	12	-	-	-	191.8	"
	12	-	-	-	359.6	"
P. compacta	13	9,700	3.2	-	-	Esler et al. 1989
P. eximia	24	-	106.0	4.4	127.5	Bond 1985
P. lepidocarpodendron	16	160	881.2	202.2	1302.3	Esler and Cowling 1990
	16	2,080	115.8	75.9	302.9	"
	16	22,480	16.3	5.5	40.6	"
P. lorifolia	20	-	82.0	33.2	153.0	Bond 1985
P. obtusifolia	17	19,400	43.4	-	-	Esler et al. 1989
P. obtusifolia	17-18	19,400	-	-	3,919	Mustart et al. 1994
P. punctata	28	-	151.0	62.7	293.5	Bond 1985
P. repens	11	-	-	-	54.5	Lombaard 1971
	12	-	-	-	75.2	"
	12	-	-	-	194.9	"
	20	-	13.0	8.3	22.0	Bond 1985
P. susannae	17-18	8,500	-	-	4,360	Mustart et al. 1994
Banksia baxteri	10/21	-	-	-	12/581	Witkowski et al. 1991
B. burdettii	15	-	448.5	187.4	832.4	Lamont & Barker 1989
B. coccinea	10/21	-	-	-	51/67	Witkowski et al. 1991
B. cuneata	15	-	-	-	968.0	Lamont et al. 1991a
B. cuneata	23	-	-	-	17,105	"
B. ericifolia	25	-	-	-	1368.0	Carpenter & Recher 1979
B. hookeriana	15	-	-	-	371.0	Enright & Lamont 1989
B. leptophylla	15	-	308.0	-	1344.0	Cowling et al. 1986
B. ornata	11	-	-	-	42.0	Gill & McMahon 1986
B. ornata	25	-	-	-	160.0	"
B. prionotes	15	-	83.0	21.0	124.0	Cowling et al. 1986
B. speciosa	10	-	-	-	27/906	Witkowski et al. 1991

Seedling mortality rates may be high (>20%), especially during the first summer after germination (Midgley 1988; Le Maitre unpublished; Mustart & Cowling 1993a,b). Data on the number of established seedlings required to produce a mature plant are sparse and may range from 3-10 or more (see Le Maitre & Midgley 1992; Chapter 3). Bond (1984) suggested that ten seedlings per adult plant may be needed to ensure population replacement. If this is accepted as a reasonable estimate, then, even if only 25% of the seeds of plants in this study produced seedlings, the number of seeds per shrub would be more than adequate for stand replacement at all ages, except for *P. repens* at site 5 (Table 3.6).

Mortality rates in stands of seed-regenerating *Protea* species tend to increase with age after reaching maximum productivity, entering a stage termed senescence (Kruger & Bigalke 1984). Bond (1980) found that the number of seedlings per parent plant was lower in senescent than mature stands. He showed that recruitment was limited primarily by low seed numbers in the senescent stand but did not investigate the source of the low numbers. This study of senescing, 28-year old *P. neriifolia* populations has provided evidence that the decline in seed numbers in senescing stands may be due decreases in both inflorescence production and seed yield per inflorescence (Table 3.6), in addition to increased parent plant mortality rates.

Several studies have shown that there is marked variation in the regeneration success of Proteaceae with canopy-stored seed - from about one seedling per parent after fires in winter to spring, to ten or more after fires in summer to autumn (Bradstock & Myerscough 1981, Bond 1984, Cowling & Lamont 1987, Midgley 1989). Two major explanations have been offered for these patterns: (a) Predation hypothesis: seed predation by small mammals during the period between seed release after fires and germination in the following winter (Bond 1984, Bond, Vlok & Viviers 1984), and (b) phenological hypothesis: seasonal variation in the size of seed banks from low in spring to high in autumn (Jordaan 1949, 1965). Bond (1985) concluded that seasonal fluctuations in seed reserves were insufficient to account for the range in seedling numbers observed in field studies. The seasonal range reported by Midgley (1989) is, however, closer to that predicted by the phenological hypothesis. While both predation and phenology are undoubtedly important factors, a species with a high rate of seed loss after seed maturation, e.g. *P. repens* (Coetzee & Giliomee 1987), would have greater seasonal fluctuation in the total seed bank than a species which accumulates many older seeds, e.g. *P. neriifolia*. Both species would show marked seasonal cycles in seed bank size when young but, as they age, *P. neriifolia* would accumulate a larger total seed bank than *P. repens* which would continue to have seasonal cycles in the quantity of stored seeds. In the senescent stage seed reserves of *P. neriifolia* would exceed those of *P. repens* at any time of year because of the high rate of seed loss in

the latter.

Marked variation in the relative recruitment success of species is a prerequisite for the coexistence of trophically equivalent species in lottery models (Chesson 1986, Cowling 1987; Bond *et al.* 1992; Laurie & Cowling 1994). *P. repens* and *P. neriifolia* differ markedly in the relationship between size and the number of seed bearing inflorescences, the number of seeds per plant and per inflorescence, and in their response to increasing stand density. These differences will influence relative seedling recruitment after fires and could, therefore, be a key factor explaining the coexistence of these ecologically similar species at many sites in Swartboskloof. This is in marked contrast to hypotheses that species segregation by microhabitat or soil suite can explain the richness of ecologically and morphologically similar species in the Cape Proteaceae (Cody 1986, Cowling 1987, Esler *et al.* 1989). Lamont and Witkowski (1995) did not find clear evidence that lottery recruitment rather than plant traits determined coexistence. It is relatively easy to study the reproductive biology of serotinous Proteaceae, and further studies on species in this family could provide key insights into the dynamics of species coexistence in the fire-prone shrublands of the Cape and Australia.

Chapter 4: A survey of the effects of seed-eating insects on seed production of *Protea neriifolia* and *Protea repens* (Proteaceae) in the Jonkershoek Valley, Western Cape Province[1]

4.1 Abstract

The effect of insects on the net seed production and seed banks of 7, 13 and 28-year old (post-fire) *Protea neriifolia* R.Br. and 28-year old *P. repens* (L.)L. shrubs was investigated in the Jonkershoek Valley. Inflorescences were harvested and divided into three age classes: the most recent crop with mature seeds (class 1), previous season's crop and all remaining seed-bearing inflorescences. Inflorescences containing seed-eating insects or frass were classed as infested. The proportion of infested *P. neriifolia* inflorescences increased from 15% in inflorescences dating from the first to 66% in those dating from the third flowering season of 7-year old plants. Thirty percent of the class 1 inflorescences of 28-year old *P. neriifolia* plants were infested compared with 56% of co-occurring *Protea repens* inflorescences. *Protea neriifolia* plants had a mean of 1.9 and co-occurring *P. repens* 10.4 seeds per insect-free class 1 inflorescence. Nearly half the insect-free class 1 inflorescences of the *P. neriifolia* plants had no seeds with a firm embryo. Low and unpredictable seed set may limit the effects of seed-eating insects on the seed yield of *P. neriifolia* when compared with co-occurring *P. repens* which has much higher and less variable seed set at the level of the individual inflorescence. In particular, a higher proportion of barren inflorescences in *P. neriifolia* may limit seed predation by reducing the likelihood that seed feeding insects locate a seed bearing inflorescence.

4.2 Introduction

Seed eating insects have a significant impact on seed production in several *Pinus* species (Mattson 1978, Forcella 1980, Schmid *et al.* 1984), *Eucalyptus baxteri* (Andersen 1989), and some *Banksia* species (Scott 1982, Cowling *et al.* 1987, Ayre & Whelan 1989). A number of seed-eating insects have been recorded in the inflorescences of several *Protea* species but only a few have a significant impact (Myburgh *et al.* 1973, Myburgh and Rust 1975, Coetzee and Giliomee 1987). About 27% of the seeds of *Protea magnifica* Link are damaged or consumed by insects between flowering and seed maturation and in older inflorescences up to 100% may be lost (Myburgh *et al.* 1974). In an intensive study of *Protea repens* (L.)L., in the same locality as this investigation, Coetzee and Giliomee (1987)

[1] Publication in preparation

found that seed losses increased from about 32% at seed maturity to 84% two years after flowering. Seed predation in *Protea lepidocarpodendron* (L.)L. varied from about 8 to 41% and was proportional to inflorescence age (Esler and Cowling 1990) and similar patterns have been observed in other Cape Proteaceae (Mustart *et al.* 1994).

Proteaceae seeds contain remarkably high concentrations of proteins and other nutrients (Pate *et al.* 1986, Esler *et al.* 1990) and so are a significant food source for vertebrate and non-vertebrate seed eaters (Bond and Breytenbach 1985) and an important nutrient sink for the plant (Pate *et al.* 1986, Esler *et al.* 1990, Witkowski and Lamont 1996). As each seed is a significant investment there should be selection for mechanisms that minimize the loss of seeds both before and after release (Bond and Breytenbach 1985). Seed survival was found to be positively correlated with variable and, to a lesser extent low seed set, in samples of inflorescences from populations of a number of *Protea* species including *P. neriifolia* (Wright 1994), but data on individual species were not presented. Mustart *et al.* (1995) found that full seeds (i.e. viable embryos) were clustered in the inflorescences and suggested that, because seed predators feed non-selectively (Coetzee & Giliomee 1987), this could enhance seed survival. The degree of clustering did not increase with increasing serotiny (duration of storage) contrary to their predictions.

Seed set in the Proteaceae seems to be generally low (Rebelo & Rourke 1986), ranging from 1.9 to 30.0% with a mean of 16.1% in 39 *Protea* species (Collins and Rebelo 1987). Seed set in *Protea repens* ranged from 27 to 30% (Coetzee and Giliomee 1987, Collins and Rebelo 1987), which is relatively high compared with 4 to 17% for *Protea neriifolia* (Horn 1962, Collins and Rebelo 1987). Large numbers of embryo-less seeds may limit seed predation where seed eaters feed non-selectively (Coetzee and Giliomee 1987), but predation avoidance mechanisms may include some indirect effects of low seed set. For example, if seed-eating insect larvae need the nutrients contained in at least one seed to complete their life-cycle (Scott 1982), then a low number of seeds could limit the numbers of these insects. Under these circumstances, plants which optimize their investment of resources in seed production by selectively aborting the seeds of whole inflorescences, rather than producing a few seed in each inflorescence, will be less subject to seed predation than those that develop at least a few seed in every inflorescence. Therefore the relatively high and consistent seed set of *P. repens*, which is equivalent to a concentration of food resources in space (Root 1973), could predispose it to higher levels of pre-dispersal seed predation than co-occurring *P. neriifolia* with lower and highly variable seed set.

The level of herbivory, by specialist herbivores, should also escalate with increasing aggregation or density, or both, of the host plant (Root 1973). A similar argument could be advanced for trends in seed abundance in time, i.e. that the level of insect infestation in the inflorescences will increase as the number of flowering seasons of a population increases. Initial infestation levels would be low because few plants flower and each produces few flowers. Infestation would depend largely on chance discoveries of inflorescences by seed-eating insects. These insects would then breed *in situ* and their populations would build up with each successive flowering season.

A sample of the inflorescences of 7, 13 and 28-year old *P. neriifolia* and co-occurring 28-year old *P. repens* was used to test the following hypotheses:

(i) The proportion of infested inflorescences of *P. neriifolia* increases with increasing age (number of flowering seasons elapsed) of the population.

(ii) The proportion of infested inflorescences in a particular year's crop increases with increasing age of the crop. This hypothesis assumes that the degree of insect infestation increases more with increasing age than it varies between successive years. This assumption is reasonable as previous studies (Myburgh *et al.* 1974, Coetzee and Giliomee 1987) have found that the proportion of infested inflorescences consistently increases with inflorescence age.

(iii) Insect infestation levels are lower in *P. neriifolia* than co-occurring *P. repens* because the latter has high seed set (Coetzee & Giliomee 1987) which makes it a more reliable food source.

(iv) Insects do not have a significant impact on the number of full seeds per inflorescence in *P. neriifolia* because the insect species do not specifically select full seeds (Coetzee & Giliomee 1987, Mustart *et al.* 1995) and thus are likely to miss the few full seeds there are in an inflorescence, especially if they are clustered (Mustart *et al.* 1995).

4.3 Materials and methods

Three sites were selected in the Jonkershoek valley, near Stellenbosch, Cape Province (Table 4.1). The plant community was an open proteoid shrubland which varied in height from 1.2 m at 7 years to 3.5 m at 28 years of age. At site 3 *Protea repens* shrubs co-occurred with *P. neriifolia* and there were a few clumps of *Widdringtonia nodiflora* (L.) Powrie (Cupressaceae), a multi-stemmed resprouting tree species up to 4 m tall, interspersed between the proteas.

The number of full seeds (those with a firm, white embryo) and the presence or absence of larvae, or insect frass, was recorded for the inflorescences of a random sample of 34 shrubs from site 1 and ten *P. neriifolia* and five *P. repens* shrubs at site 3. At site 2 the inflorescences of a sample (wandering quarter technique, Catana 1963) of 30 shrubs were collected. Sampling dates are given in Table 4.1. All seed-bearing inflorescences of each shrub were removed and placed into paper bags. The inflorescences were divided into three age classes as follows:

Class 1: most recent inflorescences with mature seeds (1985 or 1986 flowering season).

Class 2: previous crop of inflorescences (1984 or 1985 flowering season)

Class 3: all previous inflorescences which had not yet shed their seeds; these inflorescences could not be reliably subdivided into different crops from different years, especially in the 28-year old plants.

Most of the inflorescences in class 3 were three to four years old but seeds may be retained for up to seven years based on branching and counts of annual growth nodes (D. Le Maitre pers. obs.). At site 1, the shrubs first flowered in 1983 except for one shrub which had produced a single inflorescence in 1982.

TABLE 4.1: Details of the study sites in the Jonkershoek State Forest near Stellenbosch, Cape Province.

Site number	Post-fire age (years)	Aspect	Altitude (m)	Slope (deg.)	Soil parent material	Date of sampling
1	7	NE	500	17	Granite	August 1986
2	13	E	480	7	Sandstone talus/Granite	February 1987
3	28	N	500	25	Sandstone talus/Granite	January 1987

Inflorescences were classified on the basis of their position on the branches of the shrub, colour and weathering of the involucral bracts and the age of the leaves on the branch or shoot, if present. Inflorescences from the 1986 flowering season were not collected at site 1 because the seeds were not yet mature and could not be accurately sorted. The class 1 inflorescences were from the 1985 season and were therefore about seven months older than those from the other sites. This may have influenced the level of infestation but is unlikely to have altered the general trends in the infestation levels in the sample from this site. Closed inflorescences were opened by drying them in the open air or in a

forced draught oven at 30-40 °C. Seeds of *P. neriifolia* were sorted by hand (Horn 1962) and were classified as full based on their firmness and colour (Le Maitre 1990). More than 90% of these seeds germinated successfully (Le Maitre 1990). *Protea repens* seeds were too woody to classify by feel and colour and were cut open to determine the condition of the embryo.

The data on the number of seeds per inflorescence were strongly skewed so non-parametric statistics were used throughout. A generalised linear model (Proc GENMOD, SAS 1996) with a binomial distribution and a logistic link function was used to test for differences in the level of infestation between the *P. neriifolia* populations of different ages, inflorescence age classes and for differences between 28-year old *P. neriifolia* and *P. repens*. A Kruskal-Wallis test (Chi-square approximation, NPAR1WAY procedure, SAS 1985) was used to test for significant differences in the number of seeds per inflorescence between inflorescence age classes 1 and 2 of *P. neriifolia* and insect free and insect infested inflorescences within in each class.

4.4 Results

4.4.1 Insect predation levels

Insect larvae (up to 4 per capitulum) or frass were recorded in 34% of the inflorescences of 7-year old *P. neriifolia* plants. The degree of infestation increased significantly with from age class 3 to class 1 (Tables 4.2 and 4.3) as would be expected if insect populations were increasing. The trend in infestation levels in the 13 and 28-year old *Protea neriifolia* plants was the reverse of that in the 7-year old plants (Table 4.2). The increase in seed predations levels with increasing inflorescence age was significant in both of these populations (Table 4.3). The two older populations had relatively high infestation levels, suggesting that the degree of infestation had already reached a plateau. A comparison of infestation levels across stand ages showed that inflorescence age was not significant, because of the reversal in trends and that differences between ages in infestation, and the interactions between them, were not significant.

There were relatively few inflorescences in age class 3 for 28-year old *P. repens*, compared with co-occurring *P. neriifolia* (Table 4.2), because most of these inflorescences had already opened and shed their seeds, and so were excluded during sampling. Fifty-six percent of the age class 1 inflorescences, 92% of age class 2 and all of the age class 3 inflorescences in 28-year old *P. repens*, at site 3, showed some evidence of insect damage (Table 4.2). The increased in infestation with inflorescence age was significant (ChiSquare =19.73, P 0.004). Infestation levels differed significantly from those of the co-occurring *P. neriifolia* (Table 4.2 & 4.4). There were also significant differences between the species

in the way infestation levels varied between inflorescence age classes (Table 4.4). *Protea repens* shrubs do, therefore, have a greater level of pre-dispersal seed predation than co-occurring *P. neriifolia* and the infestation level increases with age to 100% of the oldest age class at this site.

TABLE 4.2. The relationship between population age, inflorescence age class and degree of insect infestation at three sites.

Post-fire age (yrs)	Species	Inflorescence age class	Number of inflorescences	Percentage with insects
7	P. neriifolia	1	72	66
		2	101	21
		3	13	15
13	P. neriifolia	1	170	46
		2	208	61
		3	176	72
28	P. neriifolia	1	88	30
		2	57	68
		3	399	59
28	P. repens	1	36	56
		2	66	92
		3	30	100

TABLE 4.3. The results of an analysis of the infestation of P. neriifolia inflorescences by insects using a generalised linear model (PROC GENMOD, SAS 1996) with post-fire age, inflorescence age class and the proportion of inflorescences infested by insects as variables (Table 4.2).

Subset	Parameter	Estimate	Degrees of freedom	ChiSquare	Probability
7-year old	Intercept	2.3984	1	21.24	<0.001
	Inflorescence age	-1.7894	1	31.75	<0.001
13-year old	Intercept	-0.7058	1	8.74	0.003
	Inflorescence age	0.5607	1	24.16	<0.001
28-year old	Intercept	-1.0653	1	11.39	0.001
	Inflorescence age	0.4951	1	17.72	<0.001
All ages	Intercept	0.1496	1	0.15	0.701
	Inflorescence age (a)	0.0341	1	0.03	0.854
	Stand age (b)	-0.0412	1	3.72	0.054
	(a) × (b)	0.0168	1	3.44	0.064

TABLE 4.4. The results of an analysis of the infestation of inflorescences of co-occurring 28-year old P. neriifolia and P. repens by insects, using a generalised linear model (PROC GENMOD, SAS 1996) with species, inflorescence age class and the proportion of inflorescences infested by insects as variables.

Parameter	Estimate	Degrees of freedom	ChiSquare	Probability
Intercept	0.4951	1	2.50	0.114
Species	1.1273	1	48.77	<0.001
Inflorescence age	0.6237	1	30.60	<0.001

Insect infestation did not have a marked impact on the number of seeds per *P. neriifolia* inflorescence, with the only significant difference being for age class 2 in the 13-year old *P. neriifolia* population (Table 4.5). The number of seeds in infested (mean = 1.45, n = 20, SE = 1.86) and uninfested (mean = 10.38, n = 16, SE = 0.85) age class 1 inflorescences of co-occurring 28-year old *P. repens* plants differed significantly (Kruskal-Wallis X^2= 14.64, $P < 0.01$). Nineteen percent of *P. repens* inflorescences without insects were barren compared with 80% of those with insect damage.

4.4.2 Seeds per inflorescence

The number of seeds per inflorescence was highly variable and strongly skewed in *P. neriifolia*. The difference between the mean and median number of seed is generally large (Table 4.5) and the coefficient of variation ranged from 139 to 303%. There were no full seeds in 42, 47 and 50% of age class 1 inflorescences at sites 1, 2 and 3 respectively, or 53, 45 and 48%, respectively, of those with no evidence of insect damage or insect larvae. The maximum number of seeds in an inflorescence of age class 1 was 88, 64, and 40 at sites 1, 2 and 3 respectively, indicating that the plants have the ability to produce large numbers of seeds per inflorescence.

The number of seeds per inflorescence only decreased significantly from age class 1 to 2 in the 13-year *P. neriifolia* population, and the decline was independent of any evidence of insect damage (Table 4.5). The high number of seeds per inflorescence in age class 2 in the 28-year old population was in marked contrast to the other data. The number of seeds per *P. repens* inflorescence in age class 1 (mean = 5.42, n=36) was significantly higher than that in age class 2 (mean = 0.62, n = 66; Kruskal-Wallis X^2 = 17.09, DF = 1, $P < 0.01$).

There was a significant positive correlation between the total number of inflorescences and the number of inflorescences with no full seeds in age class 1 in all three samples (Table 4.6). The correlation between the number of seeds and the number of inflorescences was significant only in 13-year old plants. When inflorescences with no full seeds were excluded these correlations improved and were significant at all sites. There were, however, no significant correlations between the number of inflorescences per plant and the number of seed per inflorescence, even when inflorescences with no full seeds were excluded.

TABLE 4.5. The mean and median number of full seeds per P. neriifolia inflorescence in three populations, grouped into inflorescence age classes and whether there was evidence of insect damage in the inflorescence. Different lower case letters indicate a significant difference ($P < 0.05$) in the number of seeds per inflorescence between inflorescence age classes 1 and 2 (age class 3 was excluded because it contains more than one cohort). Upper case letters indicate a significant difference ($P < 0.05$), within an age class, in the number of seeds in inflorescences with and without evidence of insect damage. The Kruskal-Wallis test (Chi-square approximation) (SAS 1985) was used to determine significant differences.

Post-fire age (years)	Age class	Number of seeds per inflorescence									
		Mean						Median			
		Insects present			Insects absent			Insects present		Insects absent	
		number	mean	SD	number	mean	SD	median	75%[1]	median	75%[1]
7	1	40	7.15	10.63aA	32	8.38	17.76aA	4	10.5	1	10.5
	2	80	4.76	6.65aA	21	5.74	9.32aA	1	9	1	8
	3	2	0.00	0.00	11	1.82	2.82	0	0	1	4
13	1	62	5.15	12.16aA	108	3.31	5.62aA	0.5	4	1	4
	2	127	0.82	2.48bA	81	1.40	3.25bB	0	0	0	1.5
	3	127	0.55	1.78 A	49	1.43	2.99 B	0	0	0	1.5
28	1	26	1.77	4.00aA	62	1.92	5.42aA	0	2	1	1
	2	39	6.03	8.57aA	18	3.28	7.97aA	2	9	0	3
	3	162	1.55	4.62 A	237	1.71	4.96 B	0	0	0	1

1: The 75th percentile; the 25th percentile was always 0.

TABLE 4.6. An analysis of the relationship between the number of seeds and the number of inflorescences in age class 1 of each P. neriifolia shrub using Spearman's rank correlation (CORR procedure, SAS 1985).

Variables	Post-fire age (years)	Sample size	Correlation coefficient
Total number of inflorescences per shrub versus:			
Number of seeds	7	20	0.41
	13	20	0.85**
	28	7	0.64
Seeds/inflorescence	7	20	0.03
	13	20	0.37
	28	7	0.04
No. of inflorescences with no seeds	7	20	0.67**
	13	20	0.86**
	28	7	0.93**
Number of inflorescences per shrub with at least 1 seed:			
Number of seeds	7	20	0.78**
	13	20	0.92**
	28	7	0.76*
Seeds/inflorescence	7	20	-0.12
	13	20	0.03
	28	7	0.65

*: P<0.05 **: P<0.01

4.5 Discussion

The data from 7-year old population support the hypothesis of a direct relationship between the proportion of inflorescences infested and the number of flowering seasons of the population. The trend in infestation levels in this sample was the reverse of that in the 13 and 28 year old plants where there was a marked increase in the cumulative degree of infestation with increasing inflorescence age. The trend in predation is in line with the increase in the number of inflorescences available for infestation and a build up in seed-predator populations (Table 4.2). These finding support the resource concentration hypothesis (Root 1973) which has also been proposed as an explanation for an increase in the percentage seed predation with increasing shrub density in *P. lepidocarpodendron* (Esler and Cowling 1990). Wright's (1994) finding that seed survival was positively correlated with variable

seed set is supported by this study as well.

The proportion of infested inflorescences increased with increasing inflorescence age except in the 7-year old population. One explanation may be that the low number of inflorescences made them harder for seed predators to locate. The infestation of older inflorescences by certain insects has been recorded for *P. repens* (Coetzee 1984) and *P. magnifica* (Myburgh *et al.* 1974) and seems to be true of the older populations of *P. neriifolia*.

Protea repens shrubs at site 3 had a higher degree of infestation than *P. neriifolia*, confirming the findings of Coetzee (1984), which were based on a much greater sample of size and different sites, that more than 90% of all *P. repens* inflorescences have evidence of insect damage by the time they are 2 years old. The differences found in this study suggest that seed-eating insects select the inflorescences of *P. repens* rather than *P. neriifolia*. Selection by insects is possible because the inflorescences of the two differ markedly in their structure, appearance and possibly in other features as well.

Insect predation generally did not have a significant impact on seed yield, or on the proportion of inflorescences without full seeds, supporting Coetzee and Giliomee's (1987) hypothesis that the insects feed non-selectively and thus do not affect seed set *per se*. A large proportion of *P. neriifolia* inflorescences have no full seeds and the number of seeds per inflorescence was very variable, whether insects were present or not, and markedly lower than in co-occurring *P. repens*. Horn (1962) also found that *P. neriifolia* had variable and low seed set (mean 3.6%, mean number of seed = 10.7, SD = 13.4, n = 35). The difference between *P. neriifolia* and *P. repens* therefore appears to be in the lower probability of an insect selecting a seed bearing *P. neriifolia* inflorescence so that insects do not have a significant impact on seed yield in the latter species. I did not examine the clustering of seeds in inflorescences and so could not test that aspect of Mustart *et al's* (1995) hypothesis. Wright (1994) did not report on whether the size of the coefficient of variation (which was negatively correlated with seed predation) was determined mainly by variation in seeds per non-barren inflorescence or by the proportion of barren inflorescences.

The lack of significant correlations between the number of inflorescences per plant and the number of seed per inflorescence, even when inflorescences with no full seeds were excluded, has important implications. A negative correlation would suggest that resources or inadequate pollen transfer limit seed set (Ayre & Whelan 1989, Copland & Whelan 1989, Whelan and Goldingay 1989) in *P. neriifolia*, but, even if inflorescences with no full seeds are excluded, there is only a weakly negative relationship for the 7-year old plants and a positive relationship in the 28-year old plants. The positive correlation between the number of inflorescences with no full seeds and total inflorescences suggests that the plants are aborting whole inflorescences rather than reducing seed yield per inflorescence.

This mechanism may also account for the finding that seed set remained constant, and possibility pre-determined, despite the reduction of the nutrient sink and thus reduced nutrient constraints, through flower harvesting in two *Protea* and two *Leucadendron* species (Mustart & Cowling 1992a). Fertilisation did not increase seeds per inflorescence although it increased inflorescence production and reduced seed mass in *Leucospermum parile* (Witkowski 1990). Pollen supplementation in four *Banksia* species did not increase the number of seed per inflorescence but did decrease the proportion of barren inflorescences in three of those species in a 'peak' flowering years (Copland & Whelan 1989). Thus a variety of observations on Proteaceae suggest that there is strong endogenous regulation of seed set at the inflorescence level although studies of other Proteaceae have found that resource limitations can be important (Stock *et al.* 1989). A number of studies have shown reductions in seed predation levels in mast flowering species compared with non-masting species (Salisbury 1942, Janzen 1971, Waller 1979, Silvertown 1980, Augspurger 1981). Barren inflorescences may act in a similar fashion by making resources for seed predators unpredictable in space rather than time, supporting Root's (1973) resource concentration hypothesis.

Is low and unpredictable seed production per inflorescence an adaptation to minimize seed predation by limiting populations of seed feeding insects (Scott 1982, Coetzee & Giliomee 1987, Collins & Rebelo 1987, Wright 1994)? There have been numerous papers about the factors which determine seed set in plants, most of which have focussed on limitations in pollen and resource supplies or genetic factors and selection patterns (Lloyd 1980, Bawa and Webb 1984, Sutherland 1986, Haig and Westoby 1988, Andersen 1989, Ayre & Whelan 1989). Different mechanisms and different combinations of mechanisms may also dominate in different taxa and many issues remain unresolved (Sutherland 1986, Shaanker *et al.* 1988, Bawa *et al.* 1989, Lyons *et al.* 1989). Limitations on the availability of critical nutrient elements (Lamont & Barrett 1988, Stock *et al.* 1989; Witkowski 1990), pollen supplies (Copland & Whelan 1989, Whelan and Goldingay 1989) and insect damage (Zammit and Hood 1986, Wright 1994) may influence seed production in some Proteaceae (see also Ayre & Whelan 1989). The data currently available show that Proteaceae embryos have more than ten times the phosphorus concentrations of leaves or inflorescence tissues (Van Wilgen and Le Maitre 1981 and unpublished data, Kuo *et al.* 1982, Jongens-Roberts and Mitchell 1986, Pate *et al.* 1986, Esler *et al.* 1990). These high concentrations suggest that there is strong selection for a few high quality seeds to give the seedling a large starting capital of nutrients and energy reserves (Pate *et al.* 1986, Stock *et al.* 1989, Stock *et al.* 1990, Mustart and Cowling 1992b, Witkowski and Lamont 1996). There is evidence that seed abortion is post-zygotic in *P. repens* (Jordaan 1944) but the mechanisms regulating seed set in *P. neriifolia* have not been studied. The primary factor determining seed set and production may, therefore, be limited resources. *P. neriifolia* may follow a bet-hedging strategy with maternal selection at the level of both the seeds and the inflorescence based on limited availability of resources, as proposed by Stock *et al.* (1989) for *Banksia laricina* (see also Ayre & Whelan 1989).

The high proportion of inflorescences which produce no seeds may serve simply as relatively inexpensive pollinator attractants (Paton 1983), pollen donors (Sutherland 1986) or decoys, or all three, with most of the nutrients invested in the tissues being recycled later (Esler *et al.* 1990). A comparison of seed set and male to female to male flower ratios in the dioecious genus *Leucadendron* and monoecious *Protea* supports the hypothesis that many inflorescences in the latter may be functionally male and simply pollen donors (Rebelo & Rourke 1986). It is clear that further studies will be needed to determine the relative importance of the various factors controlling seed set and the degree of insect infestation in the Proteaceae.

Chapter 5: Climate change and seedling recruitment of serotinous Proteaceae: a study of seed germination and seedling survival in *Protea neriifolia*

5.1 Abstract

The recruitment success of serotinous Proteaceae is influenced by a variety of factors. This experiment investigated the germination and mortality patterns of seeds and seedlings before and after an autumn fire. The data were used to develop a simple, empirical model based on indices of the daily soil moisture balance and temperature. Seed germination before the fire was similar to that after the fire but seedling mortality was higher before the fire. Seedling mortality during the first summer (October to March) after the fire was significantly correlated with the planting date, contrary to previous studies. A simple rule model derived from the data was used to test plausible climate change scenarios. A reduction of 10 or 20% in daily rainfall will have little impact on the germination of seeds released in late-summer or autumn in the western Cape, because of the long wet winter period. An increase in daily temperatures, which will also increase evaporation rates, could have a more significant impact as it reduces the length of the favourable period for germination and would increase seedling mortality during the following summer. The findings of this study support the arguments that autumn is the best time for managed fires as the seeds germinate early in the winter and the seedlings have the best chance of surviving the hot dry summer period. High seedling mortality rates during the first summer could provide the first biological indications of the adverse effects of changes in rainfall patterns and be a more sensitive indicator than trends in populations of adult plants.

5.2 Introduction

Seed germination and seedling establishment are stages in the life-cycle of a plant during which it is particularly vulnerable to the vagaries of the environment (Harper 1967, Grubb 1977, Cavers 1983, Richardson & Bond 1990). They are also critical and decisive stages in the life-cycle of the numerous fynbos species which regenerate only from seeds (Le Maitre & Midgley 1992). Many species of the Proteaceae regenerate after fires only from seeds stored on the plant in persistent woody inflorescences (cones), a seed storage syndrome termed serotiny (Lotan 1967, Lamont *et al.* 1991b). These seeds (strictly achenes) are short-lived after release so recruitment failure during the first winter almost certainly will result in local extinction. Fires in fynbos usually occur in the summer or autumn and stimulate the release of the seeds. These seeds then lie exposed to the harsh microclimate and granivores until conditions are favourable for germination. Germination results in a substantial reduction in the mortality rate as herbivory is apparently less important than granivory in fynbos (Bond 1984). Studies

of germination of Proteaceae seeds in the field have shown that germination is confined to the period from April to September (Bond 1984, Midgley *et al.* 1989, Mustart & Cowling 1993a). Similar patterns have been found in serotinous Proteaceae in Australia (Bradstock & Myercough 1981, Cowling *et al.* 1990). Vogts (1982) suggested that germination in spring might result in high mortality rates but the time of planting did not influence seedling mortality during the subsequent summer in field studies (Midgley *et al.* 1989). Seedling densities of Australian *Banksia* species increased as the length of the wet period during the winter months increased (soil moisture > 4% Specht 1981, Cowling & Lamont 1987, Bradstock & Bedward 1992). Data on seedling mortality of fynbos Proteaceae during the first summer after germination are sparse. Seedling mortality during the first summer ranged from 24% in *Protea repens* to 71% in *P. punctata* in one study (Midgley *et al.* 1989) but (Midgley 1988) reported much lower rates of about 7% in other field surveys.

5.2.1 *Seed germination*

Seeds of serotinous Proteaceae do not require after-ripening or intensive treatment such as scarification to achieve high germination rates compared with species with soil stored seeds (Van Staden & Brown 1977, Brits 1986, Le Maitre 1990). Germination on the plant is prevented by pressure from the involucral bracts which press the micropyle of the seed onto the capitulum. After release, germination depends firstly on the availability of water, and secondly on the occurrence of low temperatures (< 10 °C) either as a continuous regime or as part of a diurnal cycle. Proteaceae with soil-stored seeds appear to require fluctuating temperature regimes for optimal germination (Brits 1987, Brits & van Niekerk 1986) while seeds of serotinous *Protea* species are stimulated by low temperatures (Deall & Brown 1981, Mitchell *et al.* 1986, Le Maitre 1990, Mustart and Cowling 1991). This is not the classical cold-stratification syndrome where seeds must be subject to cold conditions to break dormancy and germination will only begin after temperatures increase again (Mott & Groves 1981). Seeds of *Protea magnifica* Link. and *P. compacta* R.Br. germinated during 'cold-stratification' at 5 °C (Deall & Brown 1981, Mitchell *et al.* 1986) although germination rates increased under the warmer temperatures (≥ 10 °C) applied later in the same experiments. Warm temperatures (> 20 °C) as a constant regime or as the minimum in a diurnal cycle appear to inhibit germination (Deall & Brown 1981, Mustart & Cowling 1991, Cowling & Lamont 1987, Bell *et al.* 1993). Optimal germination temperatures co-incided with typical temperatures during the winter germination period in three *Banksia* species (Sonia & Heslehurst 1978). Bradstock & Bedward (1992) also suggest that seed dormancy in Australian heathland Proteaceae may be imposed by high summer temperatures. The cold requirement appears peculiar as Cape fynbos generally has 30% or more of its rain in summer (Fuggle 1981) and this mechanism can delay germination of seeds and increase the period during which seeds are exposed to granivores (Bond 1984). On the other hand summer rains in the Western Cape are less predictable and are less likely to

be followed-up by further rain (Zucchini & Adamson 1984), so germination following adequate rainfall will be highly likely to result in poor establishment or seedling mortality.

Seeds of serotinous species generally germinate on the soil surface where they are exposed to short periods of drought and other adverse conditions (Lamont *et al.* 1991a, Mustart & Cowling 1993b). Seedlings emerging below the surface emerge in a relatively favourable environment in direct contact with the soil water. Seedlings emerging from seeds on the surface must be kept hydrated for long enough for the seedling's radicle to emerge (a period of at least 21 days in *P. neriifolia* Le Maitre 1990), anchor itself in the soil and begin to take up soil water. Stimulation of germination by cold conditions is strong evidence that selective pressures have favoured germination syndromes which enable them to reduce the risk of germinating after good summer rains only to die during the dry spell that would precede the next rains. The cold requirement ensures that germination only begins with the late-autumn and winter rainstorms which will, predictably, be followed by more rains. The probability of a prolonged drought following after the first rains is, therefore, low (Westoby 1980).

5.2.2 *Seedling mortality*

Seedling mortality during the first summer after a fire will be determined by the seedling's ability to establish a root system which can maintain contact with soil moisture as the surface layers dry out. Thus seedling mortality should peak in the late summer when rainstorms are infrequent and high air temperatures, incoming solar radiation and vapour pressure deficits result in high transpiration rates (Richardson & Kruger 1990, Smith & Richardson 1990) and the rapid evaporation of any rain that does fall from the soil (Smith & Richardson 1990). This pattern has been observed in one field study (Mustart & Cowling 1993a) but another field study in fynbos contradicted this prediction. Mortality was high (> 5% per month) during the periods August-October and April-June when rainfall was high and low (< 5% per month) during the drier period from December to February (Midgley *et al.* 1989); but rainfall in the southern Cape has a spring and autumn peak, reducing the length of the summer drought and berg winds in winter can result in hot and severely desiccating conditions for seedlings (Fuggle 1981). Studies of Australian Proteaceae also observed the predicted summer seedling mortality pattern and found a strong positive relationship between survival and the amount and distribution of summer rainfall (Lamont *et al.* 1991, 1993, Lamont & Witkowski 1995, Richards & Lamont 1996).

5.2.3 *Climate change*

The requirements for cold and wet conditions for successful germination also have implications for the survival of serotinous Proteas if the regional climate in the western and southern Cape changes as a result

of the current global changes. Under the current climatic regime the cold and wet requirements are coincident because cold conditions accompany the cold fronts that bring the rains but this would change if the climate changed to one of summer rainfall. However, a complete change in rainfall seasonality seems unlikely according to the predictions of current models of climate change (Hudson 1997, Joubert & Tyson 1997). The most likely scenario seems to be that mean temperatures will increase by 1-2°C in the next 50 years (Alcamo *et al.* 1994, Joubert & Tyson 1997). Minimum temperatures are likely to rise more than maximums (Easterling *et al.* 1997). Winter temperatures may also rise more than summer temperatures (Schulze & Kunz 1996). In the winter and all-year rainfall regions precipitation is likely to decrease by less than 10% and while summer rainfall will decrease by about 1% (Schulze & Kunz 1996, Joubert & Tyson 1997). Evaporation could also increase at about 3% per degree Centigrade as temperatures increase (Schulze & Kunz 1996). However, these estimates depend heavily on which model is used to estimate potential evaporation (Hulme *et al.* 1996). The south-easterly winds in summer could also increase (Schulze & Kunz 1996, Hudson 1997) and the combination will make the summer droughts longer and more severe.

Even if these predictions prove to be reasonably realistic it is very difficult to predict their actual impacts on terrestrial ecosystems and their dynamics (Walker & Graetz 1988) and the problem is compounded by the likelihood of strong vegetation feedbacks (Betts *et al.* 1997). In broad terms the most important changes are those that alter the variability (predictability) of, for example, droughts and the extreme values (Walker & Graetz 1988, Nicholls 1991, Schulze & Kunz 1996). These changes are also likely to alter the prevailing disturbance regimes, for example fire frequencies and seasonality (Swetnam & Betancourt 1990, Bond & Richardson 1990). The predicted increases in minimum temperatures could result in some protea species failing to germinate and the projected decreases in winter rainfall may affect species in marginal habitats (e.g. *Protea laurifolia* which occurs in dry fynbos). An increase in the length and severity of the summer drought could increase seedling mortality.

In this study I construct a simple empirical model based on field observations to test the hypotheses that:
- seed germination requires that moist cool conditions be maintained for a period of at least three weeks;
- seedling mortality during the first summer is directly related to the time of germination (establishment) and to the duration and intensity of the summer drought.

This model is then used to test the effects of potential effects of changing decreasing winter or summer rainfall and an increase in temperatures based on the available data on likely regional climates following global climate warming.

5.3 Methods

5.3.1 *Study site*

The study was carried out in the Swartboskloof valley near Stellenbosch in the south-western Cape. The mean annual rainfall is about 1 500 mm with 67% falling from May to September inclusive. The rainfall is high for fynbos which typically occurs in areas with about 450-1200 mm per year (Fuggle 1981). The climate is mild with mean daily maximum of 27.3 °C and minimum of 14.5 °C in February and 16.8 °C and 6.2 °C, respectively, in July (Richardson & Kruger 1990, Versfeld *et al.* 1992). The area was burnt in a managed fire on 17 and 18 March 1987, 29 years after the previous fire. The dominant community on the study sites before that fire was a tall (>2m) fynbos shrubland. Site 1 was located on a flat area with a slight northerly aspect on loamy soils derived from Cape granites. The vegetation had a closed canopy layer dominated by *Protea neriifolia* R.Br. Site 2 was located on a rocky north-facing slope on sandy soils derived from Table Mountain sandstone. The vegetation had an open canopy layer dominated by *P. neriifolia* and *Protea repens* (L.)L. and scattered clumps of *Widdringtonia nodiflora* (L.) Powrie. After the fire the study was extended to include an additional fynbos site. The vegetation at site 3 had an open canopy dominated by *Protea neriifolia* with a few *P. repens* shrubs and was close to a riverine forest community that was not burnt in the fire. An additional site (site 4) was used only in a study of natural seedling recruitment. It was situated on a steep, north-facing slope in an open shrubland dominated by *P. repens*.

5.3.2 *Seed germination & mortality*

This study was divided into two parts. In the one seeds were planted inside 14 mm mesh cages designed to exclude small mammals (henceforth exclosures) both before and after the fire. Exclosures were used to minimise the effects of seed and seedling predation on seed germination and survival patterns. The results of a separate study on the impact of seed and seedling predation by small mammals on seed and seedling survival are reported elsewhere (Botha & Le Maitre 1992). In the second part of the study four transects were laid out after the fire and the recruitment and mortality of naturally established seedlings was followed. All the *Protea neriifolia* seeds used in the seed planting experiment were hand sorted to select those with firm, healthy embryos and high viability (>90%, Le Maitre 1990).

5.3.3 *Pre-fire seed planting*

Before the fire the effect of seed planting in different seasons was tested by planting seeds in autumn, winter and spring 1986. Three pairs of large exclosures (1 m by 1 m and 0.20 m high of 14 mm diamond mesh) were set out at sites 1 and 2 on 21 April (autumn). Ten seeds were pushed 3-5 mm into the soil, radicle end downwards, inside each exclosure. The position of each seed was indicated by a wooden toothpick. Ten small exclosures (150 mm diameter and 250 mm high) were set out at each site

on 9 July (mid-winter), 21 August (late-winter) and 17 September (spring). Four seeds were planted inside each exclosure when they were set out and their positions were indicated by a toothpick. The number of seeds which germinated and the fate of seedlings was monitored at intervals of one to two months. Seedling mortality was recorded as due either to herbivory, either the shoots were removed below the cotyledons or the complete plant was consumed, or drought, if the seedling's leaves had wilted.

5.3.4 *Post-fire seed planting*

A similar experimental design was used after the fire. One planting (8 April) was monitored intensively and the remainder as often as was practical. Ten small exclosures were placed on each of seven parallel lines 20 m apart, and spaced at 5 m intervals within lines, at site 3 on 8 April 1987. The first line was inside the forest community and the second line was placed in the ecotone between the burnt shrubland and the burnt fynbos. The remaining lines were all situated in the burnt shrubland at increasing distances from the refuge. Four seeds were planted inside each exclosure as described above. Only the data for the lines in the ecotone and fynbos are analysed in detail in this study.

Five large exclosures were set out at sites 1 & 2 on 29 April and at site 3 on 8 May 1987. Twelve seeds were planted in one half of each exclosure when they were set out as described earlier. A further twelve seeds were planted in the other half of each of these exclosures on 29 May 1987. On 30 June 1987 another set of five large exclosures was set out at all three sites and twelve seeds were planted in one half of each exclosure. Twelve seeds were planted in the other half of these exclosures on 30 July 1987. Five small exclosures (150 mm diam.) were set out at each site on 21 May, 19 June, 15 July, 19 August, 10 September and 22 October 1987. Four seeds were planted inside each of these exclosures when they were set out. Seedling mortality was classified as follows: herbivory, fungal attack (damping off or discolouration of the stem primarily due to the pathogenic fungus *Colletotrichum gloeosporioides* (Penz.) Sacc.) and other causes, mainly wilting from moisture stress and seedlings which disappeared between surveys.

5.3.5 *Naturally established seedlings*

Permanently marked, one-metre wide transects were laid out at four sites. The first transect was laid out at site 2 on 25 May 1987 and was 20 m long. The transects at sites 1 and 3 were laid out on 16 July 1987 and were 10 m long. The fourth transect was laid out at site 4 on 20 August 1987 and was 20 m long. Each seedling was marked with a numbered disk fastened to the ground next to it. The seedlings were divided into the following developmental stages: emergent - seedling emerging but cotyledons not yet free of seed coat; cotyledon - cotyledons free of seed coat and unfurled but shoot bud undeveloped; cotyledons plus shoot - shoot of seedling developing; stem elongated - the stage after leaf growth when the internodes on the stem grow out. Browsing and the subsequent responses of the seedlings were noted

and the cause of mortality was classified as described in the previous section.

5.3.6 *Model for recruitment and mortality*

Seed germination in the field was compared with indices based on daily minimum air temperatures as measured in a standard Stevenson screen, daily rainfall in a standard rainguage and daily evaporation from an A-pan. The model has deliberately been kept as simple as possible to keep assumptions to a minimum and to make it useable in locations where detailed climate data are lacking. Temperature was simply summarised as the percentage of the days, between successive field observations, on which the minimum temperature was <10 °C, hereafter termed 'cool days'. This is analogous to other models which use the sum of the days below or above a temperature (degree days) to predict phenological events (e.g Kummerow *et al.* 1981). Water availability was slightly more complex. Daily rainfall is accumulated in a hypothetical soil surface layer after daily pan evaporation has been deducted from it. The soil layer is assumed to have a field moisture capacity of 10 mm of rain and any excess rainfall is drained off. The statistic used in the model is the percentage of the days, between successive observations, when the 'soil' had >0 mm of rain stored in it, hereafter termed `wet days'. A similar system was used to obtain rules relating the percentage of the seedlings which died between successive observations to the percentage wet days during that period. The model used the daily rainfall and pan evaporation records from a weather station about 0.5 km from the study area. The days which met the criteria of wet and cool during the period from February 1987 to April 1988 are shown in Figure 5.1 together with data on seed germination and seedling mortality for seeds planted on 8 April 1987.

The sensitivity of the model was tested by planting a hypothetical 100 seeds on the 15th of each month from March to October. The rules were then used to estimate seed germination and seedling mortality at monthly intervals. Total seed germination in the model was set at 100%. The climate data for the period from 1 March 1987 to 1 April 1988 were used to calculate the statistics for seed germination and seedling mortality.

Winter rainfall was decreased by reducing the daily rainfall by 10 or 20% and increasing pan evaporation by a corresponding amount. Summer rainfall could increase in two ways. If the current weather systems continue the rainfall per event could increase, if the weather systems change the number of rainy days could increase. The first possibility was simulated by increasing the actual daily rainfall from October to March by 10 or 20%. The second possibility was simulated by adding 10 or 20% more raindays with a rainfall equivalent to the current mean daily rainfall for the months from October to March. Pan evaporation was adjusted to suit. Lastly, the daily temperature was increased by 2 or 4 °C.

Seed germination is an irreversible process for most seeds. Few seeds are able to become dormant again once the initial dormancy is overcome and the embryo is metabolically active, even if conditions then

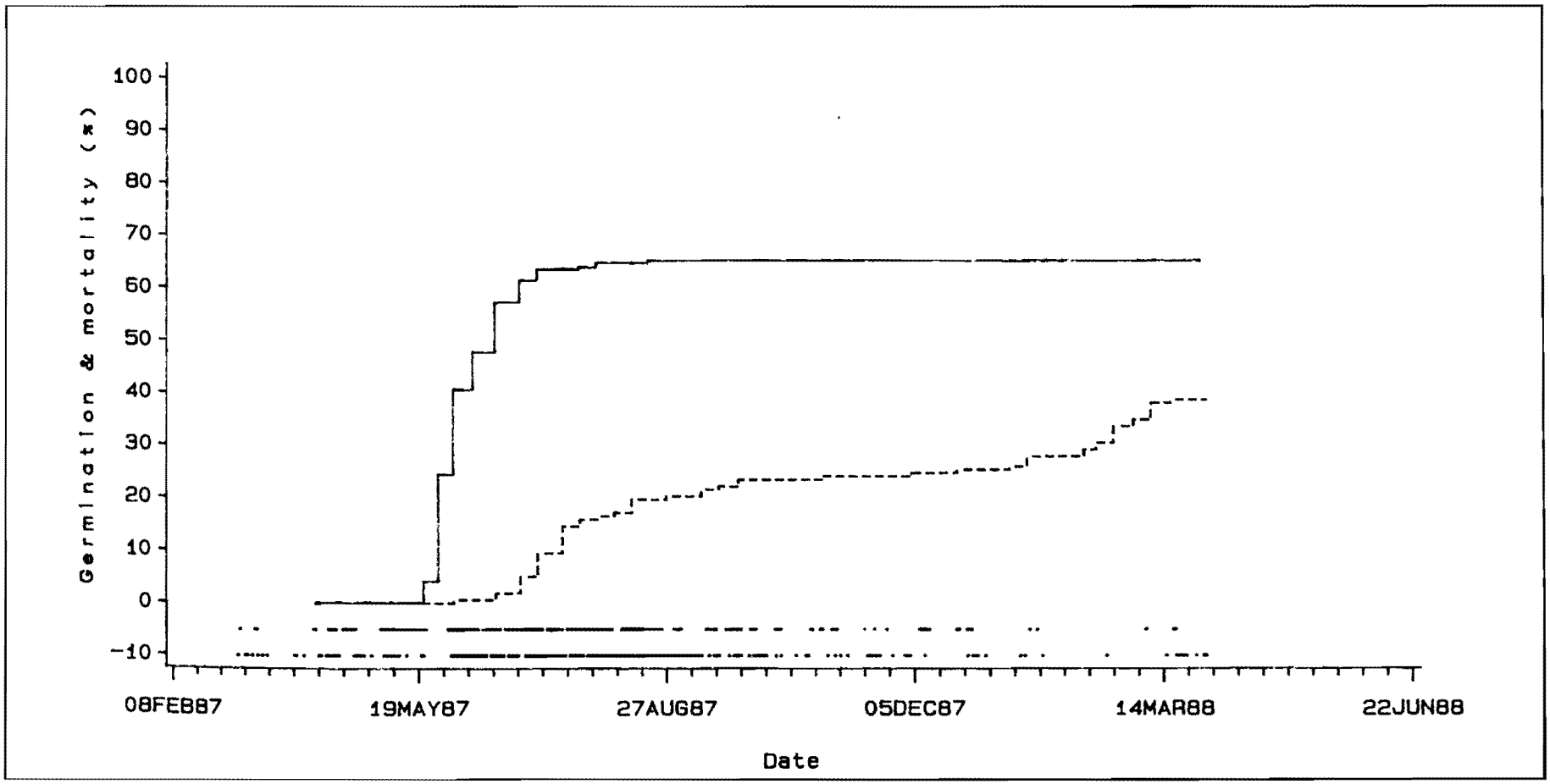

Figure 5.1 Seed germination (solid line) and seedling mortality (broken line) for seeds planted in April 1987. The broken line at -5 shows the days on which the model's soil was wet (see methods) and at -10 the days on which the minimum temperature was below 10°C (one dot on the line indicates one day, ten days per graduation on the date axis).

become unfavourable (Harper 1977, Heydecker & Coolbear 1977). If the unfavourable conditions are present for just a short period then the seeds will survive, but, if these conditions persist the seeds will die (Heydecker &Coolbear 1977). Studies of some Proteaceae show that dehydration has little impact except for one *Leucadendron* species once its radicle had emerged (Mustart & Cowling 1993b) but more studies are needed to confirm these observations. In this study the observations had, for practical reasons, to be at intervals of at least one to two weeks. To overcome the problem of germination continuing into unfavourable periods each seed planting is treated as a separate cohort and the percentage germination or mortality is compared with the percentages of wet and dry days during the current and previous interval.

5.4 Results

5.4.1 *Pre-fire seed planting*

Seed germination began about 28 days after planting (August, Table 5.1; see also Appendix 5.1) and was largely complete by 60-70 days after planting except for seeds planted in September and October. Fourteen percent of the seeds planted in September had germinated by about 34 days after planting (Table 5.1), and only one more of these seeds germinated, between 13 and 25 February 1987. Seeds planted in October also germinated during the summer (Table 5.1). A total of nine seeds germinated, four between 25 November and 2 January and four between 14 January and 13 February (Table 5.1). Total germination was highest for seeds planted on 9 July (82% Table 5.1) and was low for seeds planted in September and October, 15 and 9% respectively (Table 5.1). Cool days appeared to be relatively unimportant for germination as seeds planted in October continued germinating during January and February even though only 27% of the days had a minimum temperature $\leq 10\,^{\circ}C$.

Seedling mortality patterns were more variable than those for seed germination (Table 5.2). The highest mortality of seedlings from seeds planted on 9 April, 17 September and 20 October occurred between 26 November and 2 January but for the remainder it occurred during the period 20 October to 26 November. The percentage of wet days was low in both intervals (8-13% Table 5.2) but seeds planted in October germinated during the dry period from 26 November to 2 January (Table 5.1) while seedlings were dying. This anomaly can be explained by a closer look at the rainfall patterns. The early part of this period was relatively wet and stimulated the germination of seeds. Seed germination during this period was confined to exclosures in shady positions (D.C. Le Maitre pers. obs.). The latter part of this period was dry and resulted in the deaths of seedlings in more exposed positions.

The lowest overall mortality was recorded for seedlings from seeds planted in April (Table 5.2), with about 20% of the seedlings dying before the onset of the summer. The highest, 80%, was recorded for seedlings from seeds planted in August (Table 5.2). Only 15% of the seeds planted in September germinated and nearly 75% of those seedlings died during the summer (Table 5.2). Seedlings from the seeds planted in October also showed a high degree of turnover. Three of the four seedlings which appeared between 26 November and 2 January died before 13 February.

Table 5.1. Germination patterns of seeds planted in a 29-year old tall shrubland. Wet days are those days when there was excess moisture (see Methods) and cool days were those with a minimum temperature of 10°C or less.

Planting date (number of seeds)	Time period	Days after planting	Wet days (%)	Cool days (%)	Cumulative germination (%)	Total germination (%)
21 April (120)	21Apr-19Jun	0-60	61	60	62.9	62.9
9 July (80)	9Jul-21Aug	0-44	83	77	76.0	82.0
	22Aug-17Sep	45-71	78	70	82.0	
21 August (80)	21Aug-17Sep	0-28	78	70	11.0	60.0
	17Sep-20Oct	29-61	24	70	60.0	
17 September (80)	7Sep-20Oct	0-34	24	70	14.0	15.0
20 October (80)	20Oct-25Nov	0-35	9	47	0.0	9.0
	26Nov-02Jan	35-73	13	5	4.0	
	02Jan-14Jan	73-85	8	8	4.0	
	15Jan-13Feb	85-115	23	27	8.0	

5.4.2 *Post-fire seed planting*

The first seedlings to germinate in the post-fire plantings were recorded 22 to 23 days after planting (Table 5.3). Seeds planted on 8 April only began germinating between 30 and 44 days after planting although about half the days were 'wet' or 'cool' enough to meet the germination criteria (Table 5.3). A more detailed examination shows that cool and wet days only consistently exceeded 50% after about 20 days after seed planting (Fig. 5.2). None of the seeds planted on 29 April had germinated by 23 days

Table 5.2. Seedling mortality from October to February for seeds planted on different dates in a 29-year old tall shrubland. Wet days are those days when there was excess moisture (see section on model). Percentage mortality is calculated using the total number of seeds that germinated.

Planting date	Time period	Days after planting	Wet days (%)	Mortality (%)	Total mortality (%)
21 April	20Oct-25Nov	183-219	8	9.9	49.0
	26Nov-02Jan	220-257	13	13.2	
	03Jan-14Jan	258-269	8	3.3	
	15Jan-13Feb	270-299	23	1.3	
9 July	20Oct-25Nov	104-140	8	57.3	61.0
	26Nov-02Jan	141-178	13	2.4	
	03Jan-14Jan	179-190	8	0.0	
	15Jan-13Feb	191-220	23	0.0	
21 August	20Oct-25Nov	61-97	8	58.3	80.0
	26Nov-02Jan	98-135	13	18.3	
	03Jan-14Jan	136-147	8	0.0	
	15Jan-13Feb	138-177	23	3.3	
17 September	20Oct-25Nov	34-70	8	13.3	73.0
	26Nov-02Jan	71-108	13	40.0	
	03Jan-14Jan	109-120	8	13.3	
	15Jan-13Feb	121-150	23	6.7	
	13Feb-25Feb	151-162	8	0.0	
20 October	20Oct-25Nov	0-35	8	0.0	55.5
	26Nov-02Jan	35-73	13	33.3	
	03Jan-14Jan	74-85	8	0.0	
	14Jan-13Feb	86-115	23	22.2	
	13Feb-25Feb	116-127	8	0.0	

after planting, but 63% had germinated by 44 days after planting despite the dry conditions in that interval (Table 5.3). Continuation of germination into a dry interval also occurred in seeds planted in August. Seeds planted in August and September began germinating during an interval when less than half the days were wet (Table 5.3). But, a closer examination of the data showed that the cumulative mean wet and cool days were above 50 and 40%, respectively, for a period of 25 days during this interval (Fig. 5.3), sufficient time to stimulate germination. None of the seeds planted in September germinated between 22 October and 2 December, an interval during which wet and cool days comprised 24 and 34%,

Table 5.3. Germination rates for seeds planted in burnt fynbos after a fire in March 1987. The percentage wet and cool days is calculated for the period between the previous and the current observation. Seeds planted on 22 October did not germinate until the following winter.

Planting date	Time period	Days after planting	Wet days (%)	Cool days (%)	Cumulative germination (%)	Total germination (%)
8 April	08Apr-16Apr	0-8	50	88	0.0	65.4
	17Apr-07May	9-30	48	58	0.0	
	08May-21May	31-44	100	50	4.2	
	22May-27May	45-50	17	0	28.2	
	28May-10Jun	51-64	79	71	41.5	
29 April	29Apr-21May	0-22	82	50	0.0	79.2
	22May-29May	23-30	13	0	62.5	
	30May-19Jun	33-52	91	86	74.2	
8 May	08May-21May	0-13	100	46	0.0	78.3
	22May-29May	14-21	13	0	8.3	
	30May-19Jun	23-43	91	86	31.6	
21 May	21May-29May	0-8	13	0	0.0	80.0
	30May-19Jun	9-29	90	86	3.3	
	30Jun-03Jul	30-43	93	79	53.3	
29 May	29May-19Jun	0-21	90	86	1.7	67.2
	20Jun-03Jul	22-35	93	79	32.3	
	04Jul-30Jul	36-62	93	93	56.7	
19 June	19Jun-03Jul	0-14	93	76	0.0	83.3
	04Jul-30Jul	15-41	93	93	73.3	
	31Jul-19Aug	42-61	85	100	83.3	
30 June	30Jun-30Jul	0-30	93	93	5.6	71.1
	31Jul-19Aug	31-51	85	100	71.1	
15 July	15Jul-30Jul	0-15	93	87	0.0	80.0
	31Jul-19Aug	15-36	85	100	36.7	
	20Aug-10Sep	37-58	46	100	80.0	
30 July	30Jul-19Aug	0-20	85	100	0.0	55.6
	20Aug-10Sep	21-42	46	100	55.6	
	11Sep-22Oct	44-85	43	48	0.0	
19 August	19Aug-10Sep	0-22	46	100	0.0	70.0
	11Sep-22Oct	23-64	43	48	70.0	
	23Oct-05Nov	65-78	50	29	0.0	
10 Sept	10Sep-22Oct	0-42	43	48	41.7	41.7
	23Oct-05Nov	43-56	50	29	0.0	

respectively, of the total period. The percentage of wet and cool days was generally less than 50% after seed planting on 22 October (Fig. 5.4) and these seeds did not germinate till the following winter. More than 90% of the total germination occurred within a period of 40 to 90 days after planting and the length of the period did not vary systematically with planting date (Table 5.4, Fig. 5.5). Total germination success varied but was below 50% only for seeds planted in September (Table 5.2). Total germination success was slower in the plantings in large exclosures (29 April, 8 May, 29 May, 30 June, 30 July) than in the remainder which used small exclosures.

Table 5.4. Germination rates and the time required for germination to reach 90% or more of the total germination for *Protea neriifolia* seeds planted in burnt fynbos after a fire in March 1987 in Swartboskloof.

Planting date	Percentage germination (%)	Number of days to >=90% germination*	Total wet days (%)	Total cool days (%)
8 April	65.4	83	69	60
29 April	79.2	52	73	56
8 May	78.3	84	85	71
21 May	80.0	71	82	76
29 May	67.2	63	91	86
19 June	83.3	50	89	90
30 June	71.1	51	88	94
15 July	80.0	48	71	95
30 July	55.6	43	63	98
19 August	70.0	65	43	65
10 September	41.7	25	42	47

*: percentage of the total number of seeds that germinated.

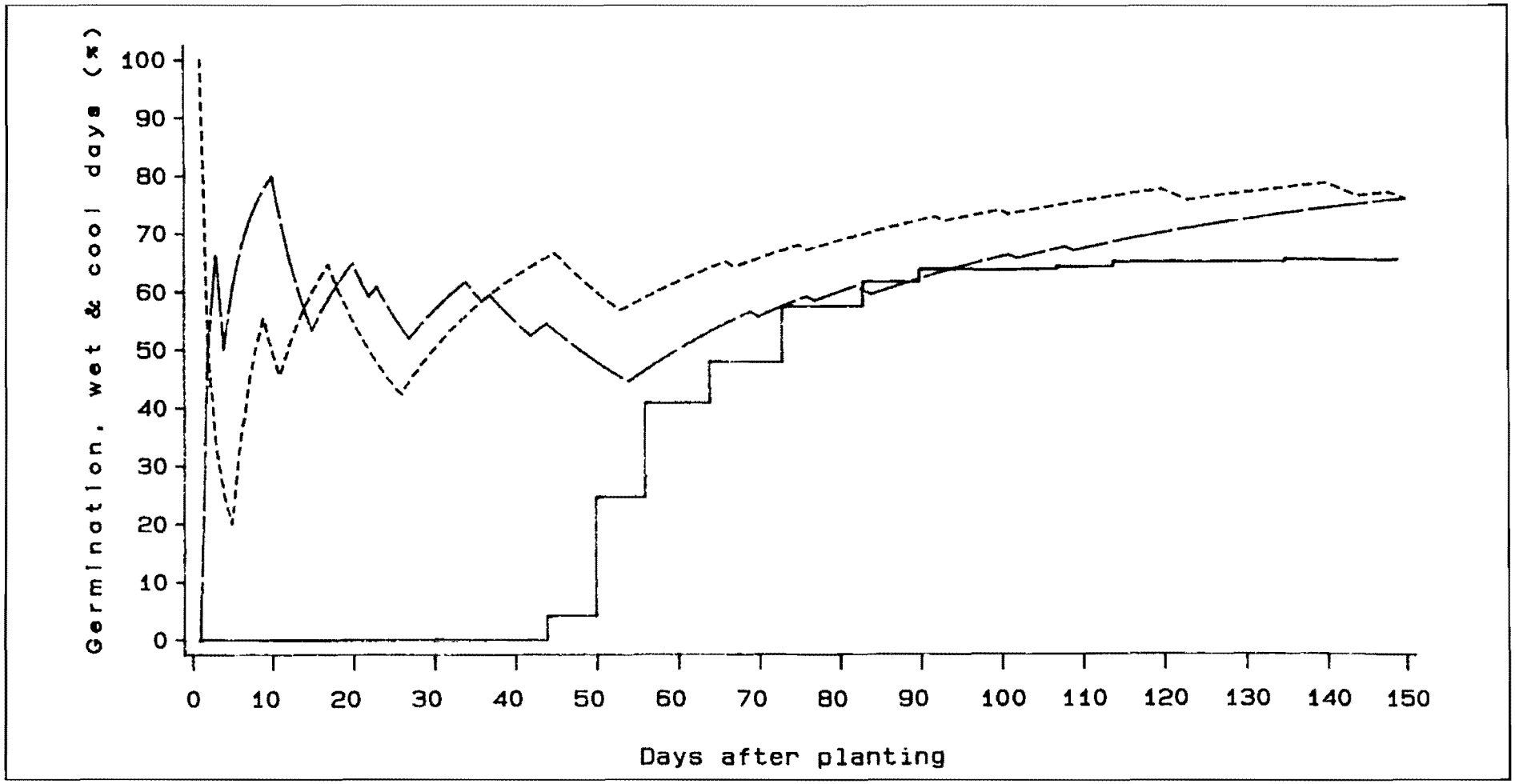

Figure 5.2 The running mean percentage of wet (dashed line) and cool days (broken line) and the cumulative percentage seed germination (solid line) for *Protea neriifolia* seeds planted on 8 April 1987.

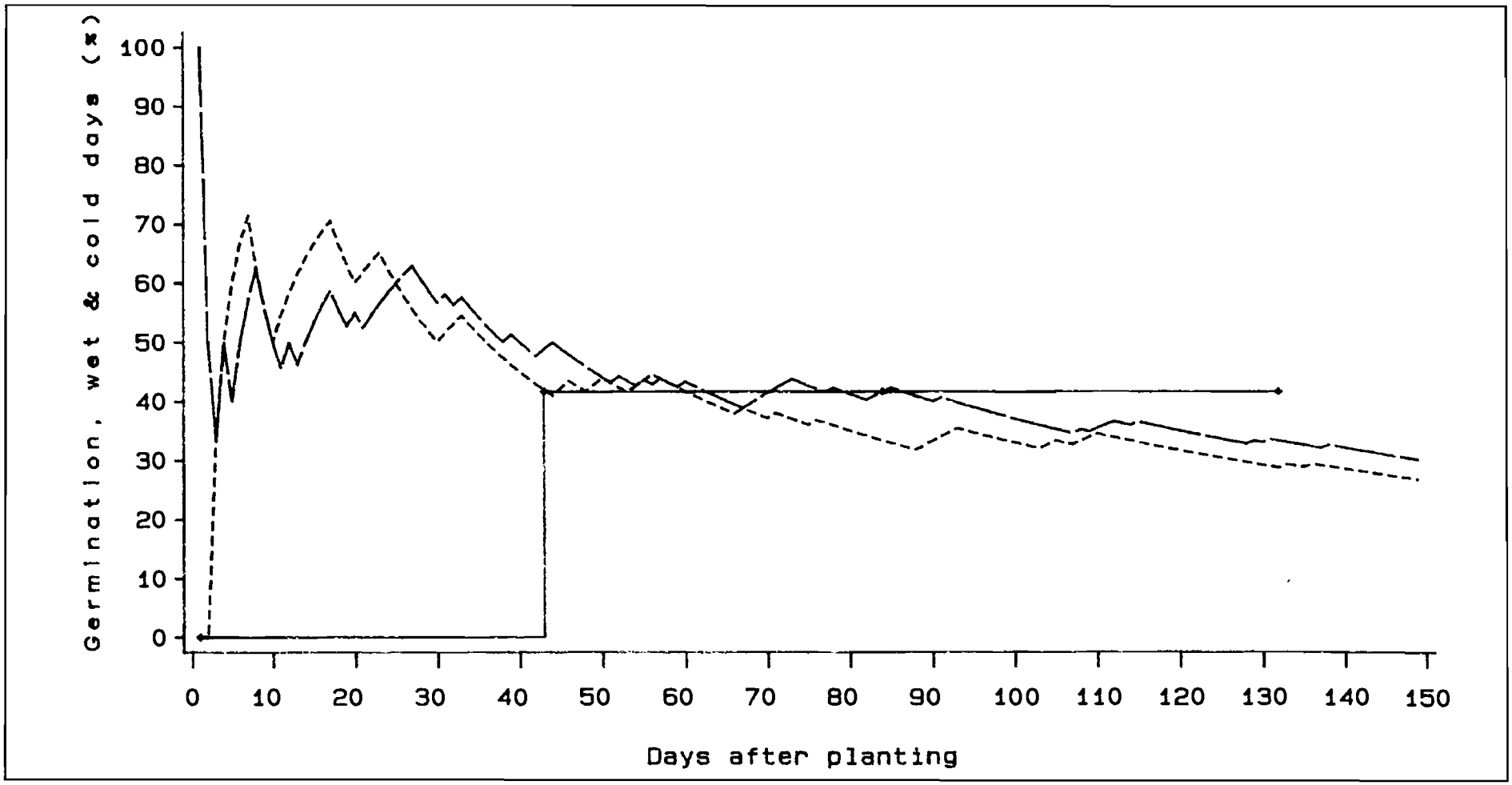

Figure 5.3 The running mean percentage of wet (dashed line) and cool days (broken line) and the cumulative percentage seed germination (solid line) for *Protea neriifolia* seeds planted on 10 September 1987.

Seedlings from seeds planted in large exclosures (29 April, 8 May, 29 May, 30 June, 30 July) had significantly higher summer mortality (between 22 October and 23 February) (mean = 60.7%, S.D. = 19.5) than those in small exclosures (mean = 39.3, S.D. = 35.6, Tukey's Studentized Range Test, $\underline{P} < 0.05$). Within each kind of exclosure the summer mortality rates increased as the planting date advanced (age at the onset of the drought decreased). In the small exclosures total summer mortality increased from 40% (8 April) to 76% (10 September) and in the large exclosures from 88% (29 April) to 99% (30 July).

Linear regressions of the percentage survival from 22 October to 23 February against age (days after planting) on 22 October gave the following relationships:

Large exclosures: Percentage survival = -21.60 + 0.4398(Days after planting)
R-square = 0.74, F = 8.49, D.F. = 1, $P = 0.06$
Small exclosures: Percentage survival = -19.79 + 0.3897(Days after planting)
R-square = 0.88, F = 29.30, D.F. = 1, $\underline{P} < 0.05$

The relationship was significant only for the small exclosures primarily because of the low mortality of the seeds planted in large exclosures on 8 May (34.1% from 22 October to 23 February) compared with the rest (mean = 67.4%). The lowest rate of seedling mortality during the summer was recorded for seeds planted on 8 April, where the total mortality from 22 October to 28 April was 15.8%. Mortality for these seedlings increased to 9% (13% of those alive on 12 February) during the dry period from 12 February to 9 March which followed a dry period from 27 January to 11 February (Table 5.5, Fig. 5.1). Mortality rates then decreased during the next interval (10-29 March) when 10% of the days were wet. The maximum mortality rates of seeds planted later in the winter also peaked during the dry period from 20 January to 23 February; up to 99% of the seedlings alive on 19 January had died by 23 February (Table 5.5).

5.4.3 *Naturally established seedlings*

Germination of seeds released after the fire in March 1987 was almost complete (>85%) by mid-July at all four sites (Table 5.6). By the 25th of May most of the seedlings at site 2 had already reached the cotyledon stage and by December most of the seedlings had reached the stage of shoot elongation (full development). Seed germination was observed during the second winter but comprised only about 5% of the total recruitment. Seedlings were quite robust and many of the browsed seedlings resprouted from

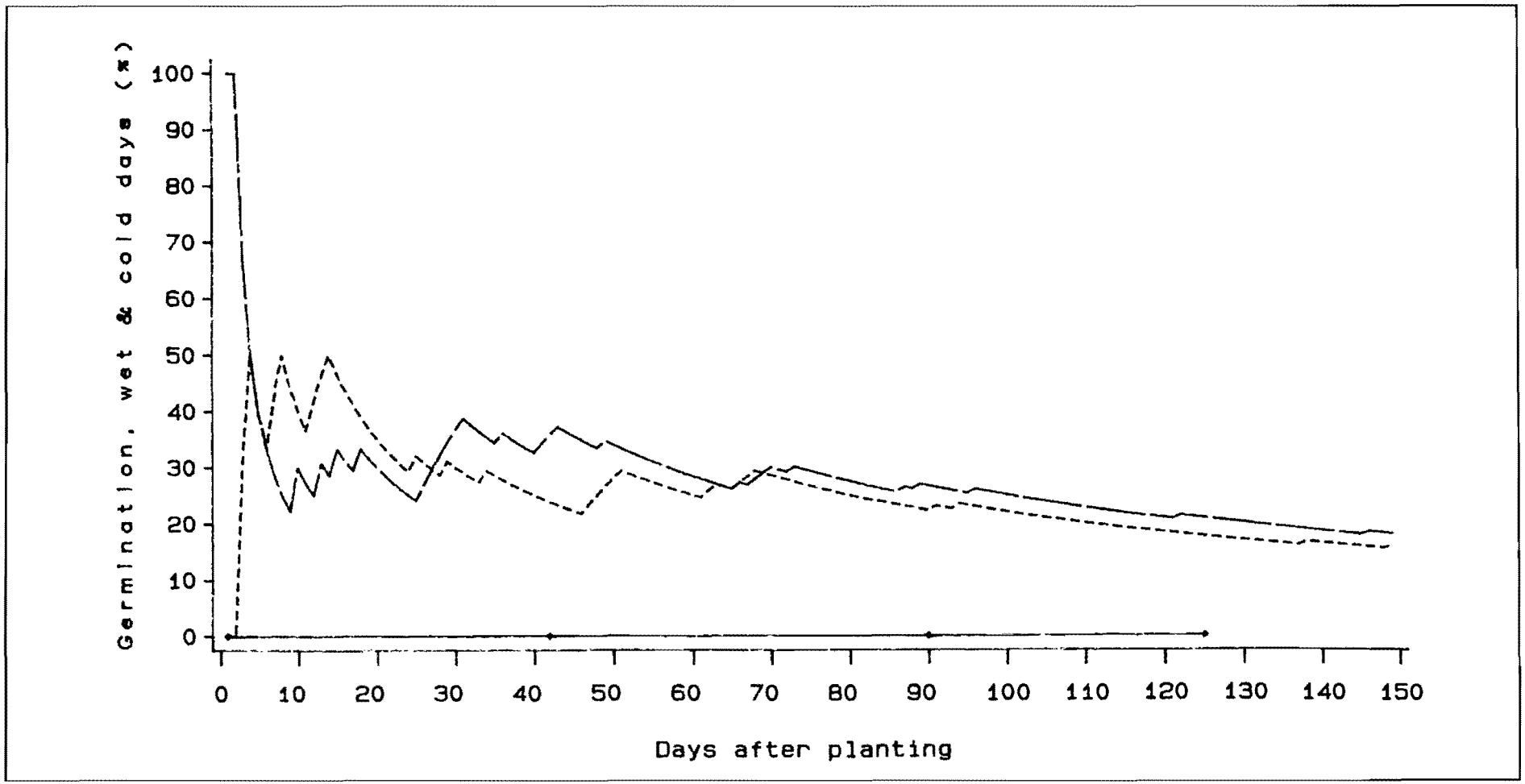

Figure 5.4 The running mean percentage of wet (dashed line) and cool days (broken line) and the cumulative percentage seed germination (solid line) for *Protea neriifolia* seeds planted on 22 October 1987.

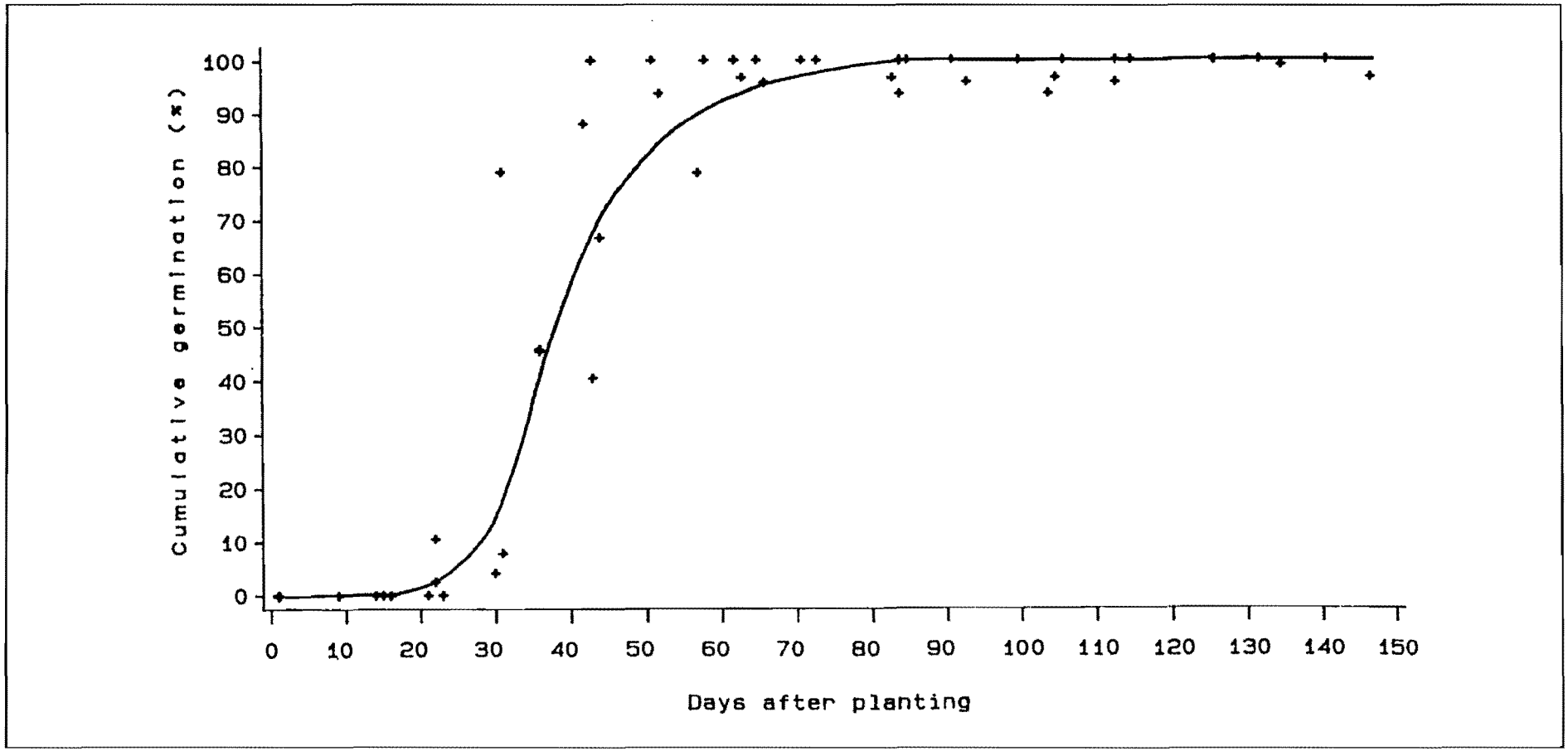

Figure 5.5 Cumulative germination of *Protea neriifolia* seeds planted after the fire in March 1987 expressed as a percentage of the total number that germinated. The smooth curve was fitted using a spline function.

Table 5.5. Seedling mortality for seeds planted in burnt fynbos after a fire in March 1987. The percentage wet and cool days is calculated for the period between the previous and the current observation. Mortality during intervals and total mortality are calculated as a percentage of the total number of seeds which germinated. Mortality during an interval is also calculated as a percentage of the seedlings alive at the beginning of that interval. Seeds planted on 22 October did not germinate until the following winter.

Planting date	Time period	Days after planting	Wet days (%)	Mortality (% of total germination)	Mortality (% of live seedlings)	Total mortality (%)
8 April	22Oct-05Nov	198-212	50	0.6	0.8	39.5
	06Nov-19Nov	213-226	14	0.0	0.0	
	20Nov-04Dec	227-241	7	0.6	0.8	
	05Dec-22Dec	242-259	33	0.6	0.8	
	23Dec-12Jan	260-280	19	0.6	0.9	
	13Jan-26Jan	281-294	14	1.9	2.6	
	27Jan-11Feb	295-310	0	1.3	1.8	
	12Feb-23Feb	311-322	0	4.5	6.3	
	23Feb-09Mar	323-337	7	4.5	6.7	
	10Mar-29Mar	338-357	10	0.6	1.0	
	30Mar-28Apr	358-388	47	0.6	1.0	
29 April	22Oct-02Dec	177-218	24	0.0	0.0	87.4
	03Dec-19Jan	219-266	21	6.3	9.0	
	20Jan-23Feb	267-301	6	51.6	80.3	
8 May	22Oct-02Dec	168-209	24	4.3	8.7	85.1
	03Dec-19Jan	210-257	21	12.8	28.6	
	20Jan-23Feb	258-292	6	17.0	53.3	
21 May	22Oct-02Dec	155-196	24	2.1	2.6	33.3
	03Dec-19Jan	197-244	21	2.1	2.6	
	20Jan-23Feb	245-279	6	10.4	13.5	
29 May	22Oct-02Dec	147-188	24	1.7	2.4	80.2
	03Dec-19Jan	189-236	21	6.6	9.2	
	20Jan-23Feb	237-271	6	45.5	69.6	
19 June	22Oct-02Dec	126-167	24	2.0	2.4	46.0
	03Dec-19Jan	168-215	21	4.0	4.9	
	20Jan-23Feb	216-250	6	24.0	30.8	
30 June	22Oct-02Dec	115-156	24	3.9	4.5	88.3
	03Dec-19Jan	157-204	21	21.1	26.5	
	20Jan-23Feb	205-239	6	46.9	80.0	
15 July	22Oct-02Dec	100-141	24	4.2	4.9	52.1
	03Dec-19Jan	142-189	21	2.1	2.6	
	20Jan-23Feb	190-224	6	31.3	39.5	
30 July	22Oct-02Dec	85-126	24	11.0	12.6	99.0
	03Dec-19Jan	127-174	21	26.0	34.2	
	20Jan-23Feb	175-209	6	49.0	98.0	
19 August	22Oct-02Dec	65-106	24	14.3	14.3	45.2
	03Dec-19Jan	107-154	21	14.3	16.6	
	20Jan-23Feb	155-189	6	16.7	23.3	
10 Sept	22Oct-02Dec	43-84	24	32.0	32.0	76.0
	03Dec-19Jan	84-132	21	20.0	29.4	
	20Jan-23Feb	133-167	6	24.0	50.0	

Table 5.6. Recruitment, development and fate of naturally recruited seedlings on transects at four sites in Swartboskloof after a fire in March 1987. The seedling stages (elong. = elongated) are described under methods. The values for mortality are cumulative. herbi = seedling killed by herbivory.

Site	Date	Live seedlings				Number browsed but live	Causes of mortality			Total number of seedlings
		Emerg-ent	Coty-ledons	Cotyl. + shoot	Shoot elong.		fungi	herbi.	other	
1	16 July 1987	3	32	35	0	0	0	0	0	70
	3 December '87	0	0	0	67	14	1	5	6	79
	13 May 1988	0	0	0	51	16	1	4	26	82
2	25 May 1987	4	31	0	0	0	0	0	0	35
	15 July 1987	21	69	97	0	2	2	5	0	194
	1 December '87	0	0	5	143	32	4	11	46	209
	13 May 1988	0	0	0	71	11	4	29	114	222
3	16 July 1987	6	65	63	0	0	0	0	0	134
	2 December '87	0	0	4	116	7	1	1	28	150
	13 May 1988	0	0	0	68	6	2	5	75	156
4	20 August 1987	3	14	8	3	0	0	0	0	28
	3 December '87	0	0	1	20	2	1	0	9	31
	13 May 1988	0	0	0	18	0	1	1	12	32

dormant buds in the axils of the remaining leaves or even the cotyledons. Seedlings which had been browsed and resprouted comprised 0.0-3.1% of the total number still alive on 13 May 1988.

Few seedlings were killed by fungi in these samples (1.2-3.1% of the total recruitment) and mortality due to herbivore browsing was low except at site 2 where it accounted for 13.1% of the total seedling recruitment, most of this between 3 December 1987 and 13 May 1988. Most of the seedlings which died disappeared between successive observations and the cause of death could not be determined. Fifty to 60% of the total mortality occurred between 3 December 1987 and 13 May 1988, with most probably dying during the drought in late January and February (Table 5.5, Fig. 5.1), except at site 4 where mortality after 3 December accounted for only 29% of the total mortality (Table 5.6). Between 37.8 (site 1) and 66.2 (site 2) of the total seedling recruitment had died by 13 May 1988.

5.4.4 *Model for recruitment and mortality*

Seeds generally only began germinating after a minimum period of about 22-23 days at least 45% of which were wet and cool (Table 5.3, Fig. 5.2-5.4). One exception was seeds planted in October before

the fire which germinated successfully during a period when 13-23% of the days were wet and 5-27% cool enough (Table 5.2). These seeds germinated only in shady sites where the litter remained moist and the temperature may have been lower than at the weather station. In the open conditions after the fire seeds planted in October did not germinate till the following winter. Seeds planted in a cool, shady forest habitat also germinated earlier than those in the open (Appendix 5.1, 1.2 versus 1.3). Another exception was seeds planted in September after the fire. These seeds probably began germinating during the first part of the period when the percentage of wet days exceeded 50 for 25 days and was complete by 22 October by which time wet days had decreased to 43% (Fig. 5.3).

The mean number of days required for 90% or more of the total germination, excluding the September planting where total germination was low (Table 5.4), was 61 (S.D. = 14). The minimum period required for 70% or more of all the seeds to germinate was about 50 days (Table 5.4). Mortality during the dry period from 20 January to 23 February (Fig. 5.1), when only 6% of the days were wet, ranged from 10-52%, 14-98% of those alive on 19 January (Table 5.5). Mortality during the previous interval, when wet days comprised 21%, ranged from 2.1-26%, 3-34% of the number alive at the beginning of the interval.

These findings were used to set the rules for the model (Table 5.7). Because seedling mortality patterns were influenced by exclosure type only data from small exclosures, which were closer to the outside conditions, were considered in deriving rules for mortality. The simulation using unchanged rainfall predicted that seed germination would begin between 15 April and 15 May and this did not change with decreased rainfall. The germination rate for seeds planted each month from March to August was 100% but only 10% of the seeds planted in September could germinate, giving a total recruitment of 610 seedlings (Table 5.8). A decrease of 10 or 20% in the total rainfall, with a corresponding increase in evaporation, resulted in the germination of only 50% of the seeds planted in August and no germination of the seeds planted in September, giving a total of 550 seedlings. The other simulated changes did not influence germination because wet days from 15 October to 15 November still did not reach the 45% threshold. With no change in the rainfall the model predicted that the total summer mortality would be 31%. A decrease of 10% had little effect but a 20% decrease increased mortality to 46%. Increased summer rainfall did not affect mortality patterns until the raindays were increased by 20%, largely because of the high evaporation rates in the summer months. An increase of 2°C in the minimum temperature decreased the germination period markedly. Cool days only exceeded 45% from 15 June to 15 September. Germination would be complete for seeds planted from 15 March to 15 July but only 50% of the August planting would germinate. The net effect would be the same as a 10 or 20% decrease

in daily rainfall. An increase of 4°C in the daily temperature would limit germination to the period 15 July to 15 September, one month shorter than with an increase of 2°C.

Table 5.7. Rules used in the model for calculating seed germination and mortality.

GERMINATION
IF number of days between seed planting and date of observation >22: **THEN**:
IF: wet days and cool days comprise ≤45% of the total: no germination
IF: wet days and cool days comprise >45% of the total
THEN: germination can begin.
IF: number of days after planting ≤30: 10% germination
IF: number of days after planting ≤45: 50% germination
IF: number of days after planting >45: max. germination

MORTALITY
IF: wet days comprised:
<25% then 2% mortality[a]
<10% then 10% mortality
<10% and the number of dry days in the previous interval was <10%
THEN: 20% mortality

a: mortality is calculated as a percentage of the seedlings alive at the beginning of the interval.

Table 5.8. The number of seeds that would germinate and seedling mortality during the first summer predicted from simulations using 100 seeds planted on the 15th of each month from March to October (a total of 800 seeds) and the rules in Table 5.7 which were derived from observed germination and mortality in the field studies (for more information see the text).

Change to daily rainfall and evaporation	Total seedling recruitment	Total summer mortality (% of predicted recruitment)	Net seedling recruitment (% of 800 seeds)
No change	610	31	53
Rainfall - 10%, evaporation + 10%	550	32	47
Rainfall - 20%, evaporation + 20%	550	46	38
Summer rainfall + 10%, evaporation - 10%	610	30	54
Summer rainfall + 20%, evaporation - 20%	610	30	54
Summer rain days + 10%, evaporation - 10%	610	30	54
Summer rain days + 20%, evaporation - 20%	610	14	66

5.5 Discussion

5.5.1 *Seed germination and mortality*

The results of the pre-fire seed planting experiment support the hypothesis that seed germination and seedling establishment between fires is constrained by factors such as seed predation by small mammals and pathogenic fungi (Bond 1984, Breytenbach 1984, Botha & Le Maitre 1992) rather than a lack of moisture or seed germination requirements. The minimum period between planting and seed germination in this experiment was about 22 days, little different from the results of laboratory experiments (Le Maitre 1990). Midgley *et al.* (1989) found that germination began after a minimum of three weeks of optimum conditions and 75% germination was achieved after about 8 weeks, about the same as that recorded in this study (Fig. 5.5). Total germination of seeds planted in August and September before the fire was lower than that after the fire (Table 5.1 & 5.3). The germination rates in this study were high, 46% before the fire (68% if September and October are excluded) and 70% after the fire, compared with the 24% recorded by Midgley *et al.* (1989) and 27% for *Protea neriifolia* near site 1 in Swartboskloof (Le Maitre 1992), but similar to the 46-79% reported by Mustart & Cowling 1993b). Low and variable recruitment (<5-39%) has also been reported for *Banksia* species in similar Australian shrublands (Gill & McMahon 1976, Cowling & Lamont 1987, Bradstock & O'Connell 1988, Lamont *et al.* 1991a). In this study the relatively cool fire (Van Wilgen & McDonald 1992) left unburnt litter and large quantities of scorched leaves so that most areas had a good cover of litter. Thus the effects of litter were pervasive and no litter versus litter-free effects on seed germination and recruitment were observed (see Enright & Lamont 1989, Lamont *et al.* 1993). Peak germination in the southern Cape study was recorded for seeds planted in May (60% Midgley *et al.* 1989) but germination success was high from April to August in this experiment (Tables 5.1 & 5.3). Germination of seeds planted in September was low (10-15%) (Midgley *et al.* 1989) compared with 42% after the fire in this experiment (Table 5.3). Seeds planted in October 1987, after the fire, only germinated in the following winter when 35% germinated (Appendix 5.1). This was still higher than the 10-28% recorded for seeds planted from September to November by Midgley *et al.* (1989).

Total rainfall in Swartboskloof during 1987 was 1671 mm and the evaporation 1652 mm, higher and lower, respectively, than the respective means (for the period 1976 to 1989 inclusive) of 1553 mm (S.D.=244.7) and 1949 mm (S.D.=150.1) (Versfeld *et al.* 1992). This is two to three times the 300 to 600 mm recorded at the sites used by Midgley *et al.* (1989). The higher rainfall in Swartboskloof would influence germination because the upper soil would remain moist for longer than under lower rainfall

reducing the risk of germination failure. Nevertheless, seed germination in Swartboskloof was also almost entirely restricted to the period from April to September so that the higher total rainfall had little effect on the seasonal spread of germination. This pattern supports the hypothesis that seed germination of serotinous Proteaceae is not simply constrained by moisture availability (Deall & Brown 1981, Bond 1984, Midgley *et al.* 1989, Mustart & Cowling 1991, Bradstock & Bedward 1992).

Mortality of seedlings in small exclosures during the first summer was higher before the fire (67%) than after the fire (49%) except for seedlings from seeds planted in September where the difference was negligible (Tables 5.2 & 5.5). The high seedling mortality in large exclosures after the fire was probably due to shading of seedlings inside the exclosure by plants which sprouted inside the exclosures but could not grow through the mesh and so formed a dense canopy (DC Le Maitre pers. obs.). Additional support for this contention comes from seeds planted in the shady forest habitat where mortality began soon after germination and 76% of the seedlings had died by mid-winter (Appendix 5.1, 1.2). Mortality before the fire was highest in the early summer (20 October - 2 January) compared with late summer (20 January to 23 February) after the fire (Tables 5.2 & 5.5), but the period from 15 January to 13 February was much wetter before the fire (23% wet days). Total seedling mortality during the summer after the fire was correlated with the date of planting contrary to the findings of Midgley *et al.* (1989). The mean mortality of seedlings in small exclosures after the fire (49%, 43% with September excluded) was high compared with most other studies. For example Midgley *(et al.* 1989) reported 31%, Midgley (1988) 7% and mortality in other *P. neriifolia* populations in Swartboskloof was 21% (Le Maitre 1992), although Maze & Bond reported 45% mortality of *p. neriifolia* at De Hoop, an area with less than 1/3 the annual rainfall of Swartboskloof. These figures are lower than those of *Banksia* species with a mean of 61-67% (range 10-100%) (Cowling & Lamont 1987, Enright & Lamont 1989, Enright and Lamont 1992) and even complete mortality (Lamont *et al.* 1991a).

At least 85% of the seeds released by *P. neriifolia* after the fire on 17/18 March had germinated by mid-July. Seed dispersal was not completed immediately after the fire as most of the seedlings at site 2 emerged between 25 May and 15 July (Table 5.6). More seedlings emerged between July and September and some, about 5%, during the second winter. The seeds which germinated in the second winter were probably dispersed after September 1987 or they would have germinated during October like the planted seeds. The staggered seed release of *P. neriifolia* supports the hypothesis that seeding species can reduce the risk of recruitment failure by spreading it over the wet season (Zammit & Westoby 1987, Le Maitre 1990) and even into the second winter. Mortality of naturally established seedlings due to

herbivory and pathogenic fungi was apparently low but many of the missing seedlings could have died of these causes and disappeared during the long intervals between observations. The overall mortality rates (38-60%) were higher than those of planted seeds but the seedlings were not protected from herbivory by exclosures.

5.5.2 *Model for recruitment and mortality*

The model used in this analysis is simple and empirical but it does give a reasonable prediction of the observed germination (Figure 5.6). The estimated mortality during the summer is lower than the observed mortality but some of the difference was due to mortality from causes other than drought (e.g. predation). Nevertheless it does provide some indications of the potential impact of changing climate. Decreasing rainfall will not have a significant impact on seed germination in Swartboskloof, largely because the conditions in mid-winter remain consistently wet enough to ensure a high percentage seed germination. Summer rainfall did not lengthen the germination period because high evaporation rates compensate for increased rainfall so that the percentage of wet days did not exceed 45%. An increase

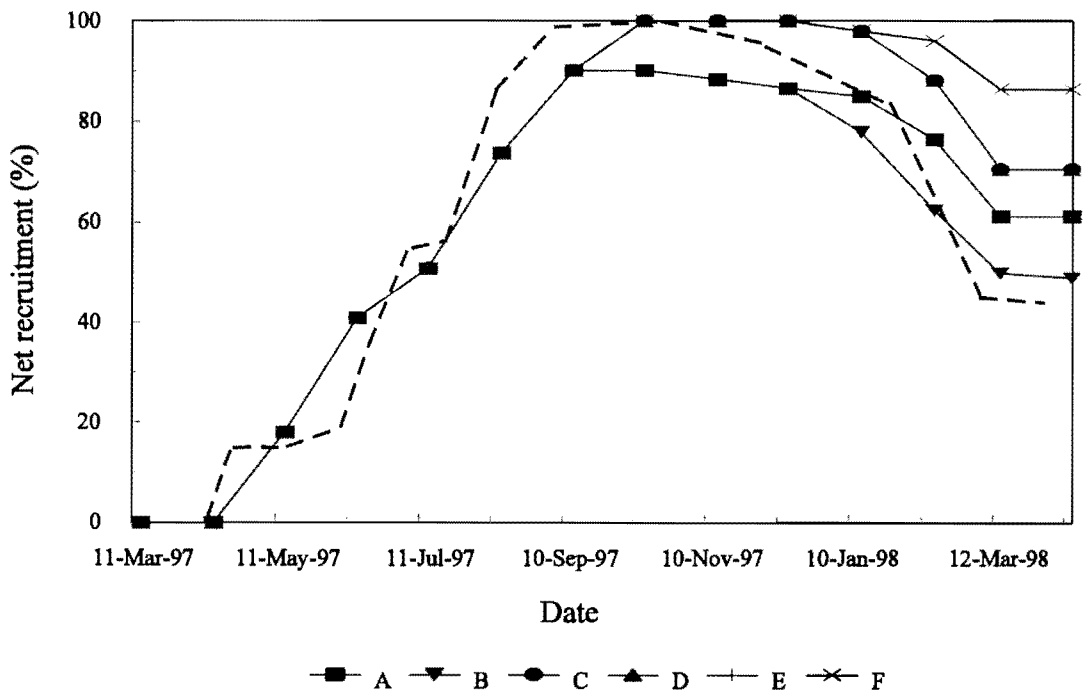

Figure 5.6 Net seedling recruitment based on field observations (dashed line) and different scenarios modelled using the rules given in Table 5.7. For scenarios the net recruitment was calculted using the maximum predicted recruitment of 610 seedlings. Net A = rainfall decreased by 10%, evaporation increased by 10%; B = as for A but altered by 20%; C = summer rainfall increased by 10%, evaporation decreased by 10%; D = as for C but altered by 20%; E = number of summer raindays increased by 10%, evaporation on raindays decreased by 10%; F = as for E but altered by 20%. The curves for C, D, and E overlap completely.

in the daily temperature reduced the length of the germination period which would increase the mortality during the following summer. The changes are unlikely to influence the mortality of mature proteas as the plants are deep-rooted and show little evidence of moisture stress even during the driest period of the summer (Kruger & Richardson 1990, Smith & Richardson 1990)

The wet and cool day criteria coincided in all the simulations except those where the daily temperature was increased, emphasising the co-occurrence of wet and cool conditions that characterise a mediterranean climate (Aschmann 1973). A decrease of 20% in total rainfall increased summer mortality, but the other changes had little impact except for a 50% reduction in mortality when the number of raindays was increased by about 20%. This latter simulation represented an effective increase of 66% in the rainfall from 15 October to 15 April. The next step would be to refine the empirical model using an established equation, such as Linacre's (1977) evaporation model, to predict the potential evaporation instead of the actual A-pan evaporation as this will give an indication of the impact of increasing daily temperatures on the occurrence of wet days.

Models based on similar studies of Australian Proteaceae have found the same kinds of patterns. Supplementary watering was suggested as the only way of maintaining viable populations of *Banksia cuneata* which experienced high to complete seedling mortality during the first summer after establishment (Burgman and Lamont 1992). For two other *Banksia* species the amount of summer rainfall was as important to successful recruitment as choosing the correct season of burn (Bradstock & Bedward 1992). All these sites had a mean annual rainfall of less than half that at Swartboskloof but they do give an indication of the potential impacts of a decrease in summer rainfall in dry fynbos (i.e. areas with less than about 750 mm of rainfall).

5.6 Conclusions

The results of this study suggest that reduced winter rainfall will have little impact on the germination of seeds released in late-summer or autumn in the western Cape, because of the long wet winter period. The changes could, however, have a significant impact in drier areas where summer conditions are more extreme and in areas on the dry periphery of different species' distributions. Seeds released in spring could be stimulated to germinate in summer but mortality during the first summer will be high. An increase in daily temperatures, which will also increase evaporation rates, could have a more significant impact. These findings support the hypothesis that germination in late-winter and spring (August-

October) can result in high mortality rates during the summer (Vogts 1982), and support the arguments that autumn is the best time for managed fires. Conditions will differ in the southern Cape where the winter rainfall season is shorter, but the summer drought may be just as severe as in the south-western Cape because much of the summer rainfall is lost through evaporation (Fuggle 1981, Midgley *et al.* 1989). Seedling mortality during the first summer can have as marked an impact on the recruitment of serotinous Proteaceae as seed predation by small mammals and loss of viability (Midgley 1989). High seedling mortality rates during the first summer, especially in populations in dry fynbos, could be the first biological indications of the adverse effect of climatic changes on fynbos plants and be a much more sensitive indicator than trends in the populations of mature plants.

APPENDIX 5.1. Summary of the data used in the development of the model of seed germination and seedling mortality in *Protea neriifolia* in Swartboskloof.

1.1 Seed germination and seedling mortality in unburnt fynbos in relation to the proportion of wet days (according to the model, see text) and cool days (minimum temperature <=10°C) during the interval between successive surveys.

Date of planting	Date of survey	Number of days after planting	Wet days (%)	Cool days (%)	Number of seeds planted	Number germinating	Cumulative germination (%)[1]	Cumulative mortality (%)[2]
21/04/86	19/06/86	60	61.0	55.9	240	151	62.9	2.6
	21/08/86	123	87.3	79.4	240	0	62.9	12.5
	17/09/86	150	77.8	70.4	240	0	62.9	15.1
	20/10/86	183	24.2	69.7	240	0	62.9	21.1
	25/11/86	219	8.3	50.0	240	0	62.9	31.0
	02/01/87	257	13.2	5.3	240	0	62.9	44.2
	14/01/87	269	8.3	8.3	240	0	62.9	47.5
	13/02/87	299	23.3	26.7	240	0	62.9	48.8
09/07/86	21/08/86	44	83.7	76.7	100	76	0.0	1.2
	17/09/86	71	77.8	70.4	100	6	82.0	1.2
	20/10/86	104	24.2	69.7	100	0	82.0	1.2
	25/11/86	140	8.3	50.0	100	0	82.0	58.5
	02/01/87	178	13.2	5.3	100	0	82.0	60.9
	14/01/87	190	8.3	8.3	100	0	82.0	60.9
	13/02/87	220	23.3	26.7	100	0	82.0	60.9
21/08/86	17/09/86	28	77.8	70.4	100	11	0.0	0.0
	20/10/86	61	24.2	69.7	100	49	60.0	0.0
	25/11/86	97	8.3	50.0	100	0	60.0	58.3
	02/01/87	135	13.2	5.3	100	0	60.0	76.6
	14/01/87	147	8.3	8.3	100	0	60.0	76.6
	13/02/87	177	23.3	26.7	100	0	60.0	79.9
17/09/86	20/10/86	34	24.2	69.7	100	14	14.0	0.0
	25/11/86	70	8.3	50.0	100	0	14.0	13.3
	02/01/87	108	13.2	5.3	100	0	14.0	53.3
	14/01/87	120	8.3	8.3	100	0	14.0	66.6
	13/02/87	150	23.3	26.7	100	0	14.0	73.3
	25/02/87	162	8.3	25.0	100	1	15.0	73.3
22/10/86	25/11/86	35	8.8	47.1	100	0	0.0	0.0
	02/01/87	73	13.2	5.3	100	4	4.0	0.0
	14/01/87	85	8.3	8.3	100	0	4.0	33.3
	13/02/87	115	23.3	26.7	100	4	8.0	33.3
	25/02/87	127	8.3	25.0	100	1	9.0	55.6

1: Calculated as a percentage of the number of seeds planted.
2: Calculated as a percentage of the number of seeds which germinated.

1.2 Seed germination and seedling mortality in an unburnt forest site after the fire in relation to the proportion of wet days (according to the model, see text) and cool days (minimum temperature <=10°C) during the interval between successive surveys.

Date of planting	Date of survey	Number of days after planting	Wet days (%)	Cool days (%)	Number of seeds planted	Number germinating	Cumulative germination (%)[1]	Cumulative mortality (%)[2]
08APR87	16APR87	9	50.0	87.5	40	0	0.0	0.0
	07MAY87	30	47.6	47.6	40	10	25.0	0.0
	21MAY87	44	100.0	50.0	40	18	70.0	0.0
	27MAY87	50	16.7	0.0	40	2	75.0	3.3
	02JUN87	56	50.0	33.3	40	0	75.0	13.3
	10JUN87	64	100.0	100.0	40	0	75.0	30.0
	19JUN87	73	88.9	88.9	40	0	75.0	53.3
	29JUN87	83	90.0	80.0	40	0	75.0	63.3
	06JUL87	90	100.0	85.7	40	0	75.0	73.3
	16JUL87	100	90.0	100.0	40	0	75.0	76.6
	23JUL87	107	85.7	85.7	40	0	75.0	83.3
	30JUL87	114	100.0	85.7	40	0	75.0	83.3
	06AUG87	121	85.7	100.0	40	0	75.0	83.3
	13AUG87	128	71.4	100.0	40	0	75.0	90.0
	20AUG87	135	100.0	100.0	40	0	75.0	90.0
	27AUG87	142	71.4	100.0	40	0	75.0	90.0
	03SEP87	149	57.1	100.0	40	0	75.0	96.7
	10SEP87	156	0.0	100.0	40	0	75.0	96.7
	17SEP87	163	71.4	57.1	40	0	75.0	96.7
	25SEP87	171	75.0	50.0	40	0	75.0	96.7
	02OCT87	178	57.1	57.1	40	0	75.0	96.7
	08OCT87	184	0.0	66.7	40	0	75.0	96.7
	15OCT87	191	42.9	28.6	40	0	75.0	96.7
	22OCT87	198	0.0	28.6	40	0	75.0	96.7
	29OCT87	205	57.1	14.3	40	0	75.0	96.7
	05NOV87	212	42.9	42.9	40	0	75.0	96.7
	12NOV87	219	0.0	14.3	40	0	75.0	96.7
	19NOV87	226	28.6	57.1	40	0	75.0	96.7
	26NOV87	233	14.3	42.9	40	0	75.0	96.7
	04DEC87	241	0.0	37.5	40	0	75.0	96.7
	10DEC87	247	66.7	16.7	40	0	75.0	96.7
	22DEC87	259	16.7	0.0	40	0	75.0	96.7
	04JAN88	272	30.8	38.5	40	0	75.0	96.7
	12JAN88	280	0.0	0.0	40	0	75.0	96.7
	19JAN88	287	0.0	28.6	40	0	75.0	96.7
	26JAN88	294	28.6	14.3	40	0	75.0	100.0
	02FEB88	301	0.0	0.0	40	0	75.0	100.0
	11FEB88	310	0.0	0.0	40	0	75.0	100.0
	16FEB88	315	0.0	0.0	40	0	75.0	100.0
	23FEB88	322	0.0	14.3	40	0	75.0	100.0
	02MAR88	330	0.0	0.0	40	0	75.0	100.0
	09MAR88	337	14.3	0.0	40	0	75.0	100.0
	17MAR88	345	0.0	12.5	40	0	75.0	100.0
	29MAR88	357	16.7	50.0	40	0	75.0	100.0
	19APR88	378	28.6	28.6	40	0	75.0	100.0
	28APR88	387	88.9	88.9	40	0	75.0	100.0

1.3 Seed germination and seedling mortality after the fire in a burnt fynbos site in relation to the proportion of wet days (according to the model, see text) and cool days (minimum temperature <=10°C) during the interval between successive surveys.

Date of planting	Date of survey	Number of days after planting	Wet days (%)	Cool days (%)	Number of seeds planted	Number germinating	Cumulative germination (%)[1]	Cumulative mortality (%)[2]
08APR87	16APR87	9	50.0	87.5	240	0	0.0	0.0
	07MAY87	30	47.6	47.6	240	0	0.0	0.0
	21MAY87	44	100.0	50.0	240	10	4.2	0.0
	27MAY87	50	16.7	0.0	240	49	24.6	0.0
	02JUN87	56	50.0	33.3	240	39	40.8	0.6
	10JUN87	64	100.0	100.0	240	17	47.9	0.6
	19JUN87	73	88.9	88.9	240	23	57.5	1.9
	29JUN87	83	90.0	80.0	240	10	61.7	6.1
	06JUL87	90	100.0	85.7	240	5	63.8	9.6
	16JUL87	100	90.0	100.0	240	0	63.8	14.7
	23JUL87	107	85.7	85.7	240	1	64.2	16.0
	30JUL87	114	100.0	85.7	240	2	65.0	16.6
	06AUG87	121	85.7	100.0	240	0	65.0	17.2
	13AUG87	128	71.4	100.0	240	0	65.0	19.7
	20AUG87	135	100.0	100.0	240	1	65.4	19.7
	27AUG87	142	71.4	100.0	240	0	65.4	20.3
	03SEP87	149	57.1	100.0	240	0	65.4	20.3
	10SEP87	156	0.0	100.0	240	0	65.4	21.6
	17SEP87	163	71.4	57.1	240	0	65.4	22.2
	25SEP87	171	75.0	50.0	240	0	65.4	23.5
	02OCT87	178	57.1	57.1	240	0	65.4	23.5
	08OCT87	184	0.0	66.7	240	0	65.4	23.5
	15OCT87	191	42.9	28.6	240	0	65.4	23.5
	22OCT87	198	0.0	28.6	240	0	65.4	23.5
	29OCT87	205	57.1	14.3	240	0	65.4	24.1
	05NOV87	212	42.9	42.9	240	0	65.4	24.1
	12NOV87	219	0.0	14.3	240	0	65.4	24.1
	19NOV87	226	28.6	57.1	240	0	65.4	24.1
	26NOV87	233	14.3	42.9	240	0	65.4	24.1
	04DEC87	241	0.0	37.5	240	0	65.4	24.7
	10DEC87	247	66.7	16.7	240	0	65.4	24.7
	22DEC87	259	16.7	0.0	240	0	65.4	25.3
	04JAN88	272	30.8	38.5	240	0	65.4	25.3
	12JAN88	280	0.0	0.0	240	0	65.4	25.9
	19JAN88	287	0.0	28.6	240	0	65.4	27.8
	26JAN88	294	28.6	14.3	240	0	65.4	27.8
	02FEB88	301	0.0	0.0	240	0	65.4	27.8
	11FEB88	310	0.0	0.0	240	0	65.4	29.1
	16FEB88	315	0.0	0.0	240	0	65.4	30.4
	23FEB88	322	0.0	14.3	240	0	65.4	33.6
	02MAR88	330	0.0	0.0	240	0	65.4	34.9
	09MAR88	337	14.3	0.0	240	0	65.4	38.1
	17MAR88	345	0.0	12.5	240	0	65.4	38.7
	29MAR88	357	16.7	50.0	240	0	65.4	38.7
	19APR88	378	28.6	28.6	240	0	65.4	39.3
	28APR88	387	88.9	88.9	240	0	65.4	39.3

1: Calculated as a percentage of the number of seeds planted.
2: Calculated as a percentage of the number of seeds which germinated.

1.4 Seed germination and seedling mortality in burnt fynbos after a fire in relation to the proportion of wet days (according to the model, see text) and cool days (minimum temperature <=10°C) during the interval between successive surveys.

Date of planting	Date of survey	Number of days after planting	Wet days (%)	Cool days (%)	Number of seeds planted	Number germinating	Cumulative germination (%)[1]	Cumulative mortality (%)[2]
29APR87	21MAY87	23	81.8	50.0	120	0	0.0	0.0
	29MAY87	31	12.5	0.0	120	75	62.5	0.0
	19JUN87	52	90.5	85.7	120	14	74.2	0.0
	03JUL87	66	92.9	78.6	120	2	75.8	4.2
	30JUL87	93	92.6	92.6	120	0	75.8	9.5
	19AUG87	113	85.0	100.0	120	0	75.8	22.1
	10SEP87	135	45.5	100.0	120	3	78.3	24.2
	22OCT87	177	42.9	47.6	120	0	78.3	29.5
	02DEC87	218	24.4	34.1	120	1	79.2	29.5
	19JAN88	266	20.8	18.8	120	0	79.2	35.8
	23FEB88	301	5.7	5.7	120	0	79.2	87.4
	21JUL88	450	55.0	60.4	120	0	79.2	88.5
08MAY87	21MAY87	13	100.0	46.2	60	0	0.0	0.0
	29MAY87	21	12.5	0.0	60	5	8.3	0.0
	19JUN87	43	90.5	85.7	60	14	31.7	0.0
	03JUL87	57	92.9	78.6	60	18	61.7	0.0
	30JUL87	84	92.6	92.6	60	7	73.3	6.4
	19AUG87	104	85.0	100.0	60	0	73.3	31.9
	10SEP87	126	45.5	100.0	60	3	78.3	36.2
	22OCT87	168	42.9	47.6	60	0	78.3	51.1
	02DEC87	209	24.4	34.1	60	0	78.3	55.4
	19JAN88	257	20.8	18.8	60	0	78.3	68.2
	23FEB88	292	5.7	5.7	60	0	78.3	85.2
	21JUL88	441	55.0	60.4	60	0	78.3	85.2
21MAY87	29MAY87	8	12.5	0.0	60	0	0.0	0.0
	19JUN87	30	90.5	85.7	60	2	3.3	0.0
	03JUL87	44	92.9	78.6	60	30	53.3	0.0
	30JUL87	71	92.6	92.6	60	16	80.0	0.0
	19AUG87	91	85.0	100.0	60	0	80.0	4.2
	10SEP87	113	45.5	100.0	60	0	80.0	10.5
	22OCT87	155	42.9	47.6	60	0	80.0	18.8
	02DEC87	196	24.4	34.1	60	0	80.0	20.9
	19JAN88	244	20.8	18.8	60	0	80.0	23.0
	23FEB88	279	5.7	5.7	60	0	80.0	33.4
	21JUL88	428	55.0	60.4	60	0	80.0	33.4
29MAY87	19JUN87	22	90.5	85.7	180	3	1.7	0.0
	03JUL87	36	92.9	78.6	180	52	30.6	0.0
	30JUL87	63	92.6	92.6	180	62	65.0	0.0
	19AUG87	83	85.0	100.0	180	0	65.0	8.3
	10SEP87	105	45.5	100.0	180	0	65.0	18.2
	22OCT87	147	42.9	47.6	180	0	65.0	26.5
	02DEC87	188	24.4	34.1	180	4	67.2	28.2
	19JAN88	236	20.8	18.8	180	0	67.2	34.8
	23FEB88	271	5.7	5.7	180	0	67.2	80.3
	21JUL88	420	55.0	60.4	180	0	67.2	83.3

Date of planting	Date of survey	Number of days after planting	Wet days (%)	Cool days (%)	Number of seeds planted	Number germinating	Cumulative germination (%)[1]	Cumulative mortality (%)[2]
19JUN87	03JUL87	15	92.9	78.6	60	0	0.0	0.0
	30JUL87	42	92.6	92.6	60	44	73.3	0.0
	19AUG87	62	85.0	100.0	60	6	83.3	2.0
	10SEP87	84	45.5	100.0	60	0	83.3	6.0
	22OCT87	126	42.9	47.6	60	0	83.3	16.0
	02DEC87	167	24.4	34.1	60	0	83.3	18.0
	19JAN88	215	20.8	18.8	60	0	83.3	22.0
	23FEB88	250	5.7	5.7	60	0	83.3	46.0
	21JUL88	399	55.0	60.4	60	0	83.3	46.0
30JUN87	30JUL87	31	93.3	93.3	180	10	5.6	0.0
	19AUG87	51	85.0	100.0	180	118	71.1	0.0
	10SEP87	73	45.5	100.0	180	0	71.1	6.3
	22OCT87	115	42.9	47.6	180	0	71.1	16.5
	02DEC87	156	24.4	34.1	180	0	71.1	20.4
	19JAN88	204	20.8	18.8	180	0	71.1	41.5
	23FEB88	239	5.7	5.7	180	0	71.1	88.4
	21JUL88	388	55.0	60.4	180	0	71.1	88.4
15JUL87	30JUL87	16	93.3	86.7	60	0	0.0	0.0
	19AUG87	36	85.0	100.0	60	22	36.7	0.0
	10SEP87	58	45.5	100.0	60	26	80.0	0.0
	22OCT87	100	42.9	47.6	60	0	80.0	14.6
	02DEC87	141	24.4	34.1	60	0	80.0	18.8
	19JAN88	189	20.8	18.8	60	0	80.0	20.9
	23FEB88	224	5.7	5.7	60	0	80.0	52.2
	21JUL88	373	55.0	60.4	60	0	80.0	52.2
30JUL87	19AUG87	20	85.0	100.0	180	0	0.0	0.0
	10SEP87	43	45.5	100.0	180	100	55.6	0.0
	22OCT87	85	42.9	47.6	180	0	55.6	13.0
	02DEC87	126	24.4	34.1	180	0	55.6	24.0
	19JAN88	174	20.8	18.8	180	0	55.6	50.0
	23FEB88	209	5.7	5.7	180	0	55.6	99.0
	21JUL88	358	55.0	60.4	180	0	55.6	100.0
19AUG87	10SEP87	23	45.5	100.0	60	0	0.0	0.0
	22OCT87	65	42.9	47.6	60	42	70.0	0.0
	02DEC87	106	24.4	34.1	60	0	70.0	14.3
	19JAN88	154	20.8	18.8	60	0	70.0	28.6
	23FEB88	189	5.7	5.7	60	0	70.0	45.3
	21JUL88	338	55.0	60.4	60	0	70.0	45.3
10SEP87	22OCT87	43	42.9	47.6	60	25	41.7	0.0
	02DEC87	84	24.4	34.1	60	0	41.7	32.0
	19JAN88	132	20.8	18.8	60	0	41.7	52.0
	23FEB88	167	5.7	5.7	60	0	41.7	76.0
	21JUL88	316	55.0	60.4	60	0	41.7	84.0

Date of planting	Date of survey	Number of days after planting	Wet days (%)	Cool days (%)	Number of seeds planted	Number germin-ating	Cumulative germination (%)[1]	Cumulative mortality (%)[2]
22OCT87	02DEC87	42	24.4	34.1	60	0	0.0	0.0
	19JAN88	90	20.8	18.8	60	0	0.0	0.0
	23FEB88	125	5.7	5.7	60	0	0.0	0.0
	21JUL88	274	55.0	60.4	60	21	35.0	0.0

1: Calculated as a percentage of the number of seeds planted.
2: Calculated as a percentage of the number of seeds which germinated.

Chapter 6: Fires and plant life histories: an application of Clark's (1991) models for seeders and sprouters to fynbos Proteaceae

Summary

Life-history theory has been able to explain patterns in the observed life-histories, growth and resource allocation in many organisms and in different environments. One of the areas of difficulty has been in finding a suitable basis for modelling the life-histories of species in disturbance driven environments because many of the standard assumptions of life-history theory (e.g. that there is continuous recruitment) are violated. Clark (1991) developed models which accommodate these violations of standard life-history theory and also establish a direct relationship between the fire frequency distributions and the age at first reproduction of fire-killed (seeder) and fire-surviving (sprouter) species given that there is a close correlation between age at first reproduction and the lifespan. The models assume that seeding species maximise the probability of being mature at the time of a fire while sprouting species maximise the number of reproductive opportunities during their lifetime. These models were tested using fire frequency data for a number of areas in the fire-prone shrublands (fynbos) of the Western Cape, South Africa, and information on the age at first reproduction, mortality rates and lifespans of a number of Proteaceae species. Maximum likelihood methods were used to fit probability distributions to the data and showed that distributions with an increasing probability of a fire with increasing post-fire age (Gamma, Weibull) were more appropriate than the Exponential distribution which assumes a constant probability of a fire. The predicted juvenile periods of *Protea neriifolia,* a seeder with mean annual mortality rates of about 5.6% - based on the Gamma distribution - were close to those observed in field studies. The predictions for *Orothamnus zeyheri*, a seeder with a relatively high mean mortality rate of 14.8% were much shorter than the observed five years except where there was a low probability of a fire in young vegetation. Predicted juvenile periods based on the Exponential distributions were generally shorter than observed, largely because the Exponential distribution overestimates the probability of a fire in young vegetation. The predicted juvenile periods for *Protea nitida*, a sprouter which is relatively fire-sensitive as a seedling or sapling, underestimated the likely primary juvenile period of at least 15 years. The models are sensitive to both the magnitude of the estimated of the mortality rate (particularly the sprouter model) and the ratio of the juvenile period to the lifespan. Clark's models appear to hold for fynbos seeders and sprouters. His assumption that sprouters and seeders are following different life-history strategies is supported by a number of other lines of evidence, both physiological and demographic.

6.1 Introduction

One of the issues that has intrigued students of life-history theory is the question of how often an organism should reproduce during its lifespan (Cole 1954; Charnov & Shaffer 1973; Stearns 1976, 1989). In general organisms can be divided into two major groups - those that reproduce only once (semelparous) and those that reproduce more than once (iteroparous). Those that reproduce only once essentially can invest all the available resources in offspring, those that do not must invest a proportion of their resources in growth and persistence. This is analogous to the distinction between sprouters and seeders in fire-prone communities - sprouters invest in surviving fires and can recruit several cohorts of seedlings; seeders do not invest in surviving fires and effectively recruit only one cohort of seedlings as recruitment between fires is rare or non-existent. These differing resource allocation patterns are evident in several reproductive traits (Keeley & Keeley 1977; Carpenter & Recher 1979). Seeders produce more seeds (Keeley 1977; Hansen *et al.* 1991), accumulate larger seed banks (Keeley & Keeley 1977; Cowling *et al.* 1987; Meney *et al.* 1994), have higher seed germination percentages and seedling recruitment (Keeley & Zedler 1978; Le Maitre 1992), more rapid seedling growth and higher seedling survival rates (Keeley & Zedler 1978; Zammit and Westoby 1987b, Parker 1984), higher moisture stress resistance (Keeley 1986; Groom & Lamont 1995; Richards & Lamont 1996), and maintain little or no energy reserves in the form of starch (Pate *et al.* 1990, 1991).

6.1.1 Lifespans and juvenile periods

A few studies have examined another potential life-history trade-off - that between the period from birth to first reproduction (juvenile period) and longevity. Studies of a wide variety of plant species have shown that the duration of juvenile periods and lifespans are directly related (Harper & White 1974; Loehle 1988). In order to live long trees have to invest, for example, in more and stronger structural tissues and defences against pathogens; this results in delayed reproduction (Loehle 1988). An analysis of data for a wide range of trees found that for angiosperms the duration of the juvenile period is about 0.19 times the lifespan; for gymnosperms it is about 0.16 (Loehle 1988, Clark 1991).

Van Wagner (1978) and Johnson (1979) described fire recurrence intervals by fitting probability distribution and providing interpretations for the fitted parameter values (see also Yarie 1981, Johnson & van Wagner 1985, Johnson & Gutsell 1994). Johnson (1979) also suggested that fire recurrence distributions indicative of frequent fires would favour r-selected life-histories and infrequent fires K-selected life-histories. Clark (1991) extended this thinking and tested whether age

to first reproduction in fire-surviving (sprouter) and fire-killed (seeder) pine species differed as expected given the prevailing probability distribution of fire recurrence intervals in their native habitat. He hypothesised that: (a) the optimal seeder life-history **maximises the probability of being reproductively mature** when the next disturbance occurs; this is based on the observation in many studies that failure to achieve reproductive maturity before the next disturbance results in extinction; and (b) the optimal sprouter life history would **maximise the number of recruitment opportunities** during the lifespan. For seeders the predicted maturation time was predicted to vary with the mortality (thinning) rate - at low rates age at reproductive maturity (t_1) was ≈ 0.4 x (expected disturbance interval in years); at high rates $t_1 \approx 0.4 \div$ (mortality rate per year). For sprouters the predicted maturation time was determined by the susceptibility of juveniles to fires and the trade-off between maturation and longevity. The predicted maturation time (based on the probability of reproduction) for a seeder, *Pinus contorta,* and a sprouter, *P. resinosa,* closely matched their recorded maturation times of 25 and 55 years (Loehle 1988), respectively.

6.1.2 A life-history model for disturbance driven environments

Recruitment and mortality in many sessile organisms are tightly linked to the disturbance regimes in their environments (Clark 1991). This coupling has resulted in the evolution of life-histories which differ significantly from those employed in standard life-history models (Stohlgren and Rundel 1986; Bond 1987; Hilbert 1987; Grubb 1988; Clark 1991, Le Maitre & Midgley 1992):

Episodic recruitment with cohort thinning between recruitment events: In fire-prone shrublands recruitment is essentially confined to the first wet season after a fire except for 'obligate sprouters' (Keeley 1986; Le Maitre 1992). This differs from conventional life-history models where there is no delay between seed production and recruitment of seedlings. Populations thus comprise discrete cohorts rather than having a continuous recruitment and thus a continuous age distribution (Stearns 1976, 1977; Hilbert 1987; Laurie & Cowling 1994). The number of individuals in a cohort decreases relatively rapidly in the first one or two years after establishment and more slowly thereafter, sometimes increasing again as the plants near the end of their lifespan (Gill & McMahon 1986; Montygierd-Lloyba & Keeley 1987; Clark 1991; Le Maitre 1992; Bond & van Wilgen 1995; Mustart & Cowling 1993a; Maze & Bond 1996; Chapters 2 & 5).

Delayed maturity: In many life-history models there is no allowance for a delay between recruitment and reproductive maturity. This is appropriate for an environment where there is no delay between seed production and recruitment because delayed maturity is a key constraint on population growth

rates (Levins 1966; Caswell 1982). But where recruitment depends on disturbances there can be considerable advantages in delaying maturity, especially where a long lifespan may be required or net fecundity increases substantially (Cohen 1968; Schaffer and Gadgil 1975; Stearns 1976; Harper 1977; Gill 1978; Southwood 1988). Delayed maturation is common in woody fynbos species and many Proteaceae mature between 4 and 8 years (Williams 1972; Kruger & Bigalke 1994; Chapters 2 & 3)

Carrying capacity: A key axiom in many life-history models, for example the r-K selection model (MacArthur & Wilson 1967), is that environments have a limited carrying capacity. Most life-history models assume an "average" competition intensity. While this may be appropriate for animals which can adjust their spacing and resource-use patterns in response to competition for resources, it is incorrect for sessile organisms such as plants which are locked into local (patch) densities and interactions and compete for essentially the same set of resources (Bradshaw 1972; Schaffer & Leigh 1976; Grubb 1977; Harper 1977; Pacala 1988). In addition, the intensity of competitive interactions will change at the local scale as plants increase in size; eventually this leads to self-thinning (Harper 1977).

6.1.3 Clark's life history model

The model developed by Clark (1991) incorporates the realities described above and is built around three basic relationships:

A*ge-specific mortality*: To make the model tractable a constant mortality rate is assumed; this differs from the commonly observed pattern of higher mortality rates in juveniles and during senescence (e.g. Le Maitre 1992) but is typical of the majority of the lifespan (Clark 1991). In mathematical form this is represented by the negative exponential distribution:

$$S(t) = e^{-\lambda t}$$

where S(t) is the survival function, t = time, e = is the base of natural logarithms (≈2.17828) and λ = the mortality rate per unit time.

Juvenile period and lifespan: Following Loehle (1988) the juvenile period (t_1) is proportional to the lifespan (t_2) i.e. $t_1/t_2 = b$ where b is a constant. Clark (1991) uses $\alpha$where $\alpha = 1/b = t_2/t_1$ and thus $t_2 =$

$t_1\alpha$. The reproductive period, R, from t_1 to t_2 therefore is expressed mathematically as:

$$R=t_2-t_1=t_1(\alpha-1)$$

A probability distribution of disturbances in time: The probability of a disturbance is a function of the time since the last disturbance; Clark (1991) examined three different forms of probability density functions - Exponential, Gamma and the Weibull. All three were examined in this study.

The Exponential distribution assumes a constant probability of fire; the cumulative probability density function has the following form:

$$F(t)=1-e^{-\lambda t}$$

where t is the time interval, e is the base of natural logarithms (≈2.17828) and λ is the probability of an event, in this case a fire.

The Gamma distribution allows the probability of fire to change with increasing post-fire age of the vegetation; the cumulative probability density function has the following form:

$$F(t)=1-\frac{e^{-\lambda t}}{\Gamma(c)}$$

where the symbols are the same as above, c = a dimensionless shape parameter and $\Gamma_{(c)}$ = the Gamma function.

The Weibull distribution also allows the probability of a fire to change with time. It is more flexible than the Gamma function and therefore has often been used for fire recurrence interval analysis (Clark 1989). It has the following form when expressed as a cumulative probability density function (Clark 1989; Cohen 1965):

$$F(t)=1-e^{-(\lambda t)^c}$$

where λ is also called the scale parameter and c the shape parameter. If c = 1 then the Weibull is the same as the Exponential, if c < 1 then the probability of an event decreases with time and if c > 1 then the probability increases with time.

In this paper I wish to test the predictions of these models about the length of the juvenile periods of seeders and sprouters using data on fire recurrence intervals and life history data for *Protea neriifolia* (serotinous seeder with short-lived seeds) and *Protea nitida* (sprouter).

6.1.4 Seed banks

In addition I examined the implications of seed banks for the predicted life-histories of seeders. Clark (1991) recognised the importance of seed banks but did not include them, primarily to keep his model as simple and general as possible. This is a key weakness in Clark's model because fitness should be measured by the number of offspring that survive to reproduce (see Cody 1966) rather than whether or not the parent has opportunities to reproduce. Studies of seed banks have shown that there are a range of seed storage strategies and seed bank dynamics. I intend to focus on just two: long-lived seed banks that can outlive the parent plant and short-lived seedbanks that (typically) persist less than a year after parent mortality. Serotinous Proteaceae are a good example of the latter, while ant-dispersed proteas are an example of the former. Seeds of the ant-dispersed *Orothamnus zeyheri* germinated following a fire 19 years after the last living plants were seen on that site (Boucher 1981). Long-lived seed banks like this significantly increase the effective lifespan of the plant (Cohen 1968; Clark 1991). This allows for increased investment in reproduction and a corresponding reduction in the vegetative lifespan. This line of argument suggests the following hypotheses about the relationship between age-specific mortality and seed banks in seeders that depend on post-fire recruitment. For the same probability distribution of fire frequencies:

- species with seeds that are short-lived after the death of the parent plant should maximise their lifespans to ensure they persist until a fire is virtually certain. The high costs of investing in the structures and defenses needed to ensure longevity (see Loehle 1988) would result in delayed reproductive maturity, low mortality rates and marked senescence;
- species with seed banks that can persist for a number of years following dispersal need not invest as much in the structures needed to ensure longevity and thus should have precocious reproduction, higher mortality rates and little indication of senescence; thus their lifespans should be shorter than those of serotinous species.

6.2 Methods

6.2.1 Study sites

This study combines data on fires from several different sites in the Western Cape Province, South Africa in order to get fire history data for a range of sites. The climate is Mediterranean with 65-80% of the rainfall in the winter half year in the west to bimodal in the east. The Cederberg Mountains are situated about 180 km north of Cape Town (32°22' S, 19°7' E) and are about 67 240 ha in extent (Brown *et al*.1991). Table Mountain (5 700 ha) is immediately south of Cape Town (33°59' S, 18°25' E) (Richardson *et al.* 1994). Swartboskloof (373 ha) is situated in the Jonkershoek valley 30 km east of Cape Town (33°57' S, 18°55' E) (Van Wilgen & McDonald 1992). The Kogelberg State Forest (34 400 ha) is about 50 km east of Cape Town (32°20' S, 19°3' E) (Richardson *et al.* 1994). Jakkalsrivier is situated in the Groenland Mountains 15 km north of the Kogelberg and is about 200 ha in extent. The Kamanassie Mountains (27 989 ha) are situated about 450 km east of Cape Town (33°40' S, 22°45' E). All the areas have mountain fynbos vegetation with some communities dominated by tall shrubs of the Proteaceae. *Protea neriifolia* occurs at Swartboskloof, Kogelberg and Jakkalsrivier. The ecologically similar *P. laurifolia* is widespread in the Cederberg and *P. lorifolia* in the Kammanassie Mountains. *Protea nitida* occurs in all these areas except the Kammanassie while *Orothamnus zeyheri* only occurs in the Kogelberg area.

6.2.2 Fire recurrence interval data

Although there have been a number of studies of fire regimes in fynbos (e.g. Horne 1981), only a few studies have provided quantitative data on fire recurrence intervals for fynbos. The information used in this analysis was taken from the data collected the following studies: Brown *et al.* (1991) for the Cederberg Mountains; Van Wilgen & McDonald (1992) for Swartboskloof; and Richardson *et al.* (1994) for the Kogelberg, Table Mountain and Kammanassie Mountains. All recurrence interval data were derived from maps of fires compiled over a periods of 15 or more years. Data for the Cederberg were derived from a systematic point sample and for the other sites from a GIS database containing digitised fire maps. Parts of Table Mountain have been protected from fire for 48 and 92 years by human intervention (Richardson *et al.* 1994); these were excluded from this analysis. Kruger (1979) presented a hypothetical curve for the cumulative probability of fire with increasing post-fire age in fynbos. A similar curve was constructed by Richardson *et al.* (1994) as the ideal fire recurrence interval distribution for fynbos managers to aim at achieving; this distribution is called the 'desired' in this study.

6.2.3 Age to first reproduction

Data on the age at first reproduction were taken from the following studies: Le Maitre (1992) and Chapters 2&3 for *Protea neriifolia*; Le Maitre (1992) for *Protea nitida*, and Boucher (1981) and Le Maitre *et al.* (1991) for *Orothamnus zeyheri*. Clark (1991) provided the following approximations for estimating the age at first reproduction based on the parameters of the probability distributions. For seeders the juvenile period that will maximise the probability of being mature when a fire occurs for the Exponential distribution is:

$$t_1^* = \frac{A}{\lambda_s + \lambda_p}$$

where t_1^* is the age at reproductive maturity, $A = \ln(\alpha)/(\alpha-1)$, λ_p is the mortality rate, λ_s is the probability of a fire and α is the inverse of the ratio of the age at reproductive maturity (t_1) to the lifespan (t_2), i.e. $\alpha = t_2/t_1$. Clark (1991) calculated from data provided by Loehle (1998) that for Angiosperms the value of α is about 5.4 and thus that $A = 0.39$.

For the Gamma distribution the equivalent equation is:

$$t_1^* = \frac{cA}{\lambda_s + \lambda_p}$$

where c = the shape parameter of the gamma probability distribution.

For sprouting species the renewal functions have to be used to derive the optimal juvenile periods. This is apparently only possible for the Exponential distribution as the renewal function for both the Gamma and Weibull distributions does not have a closed form (Cox 1962). For a sprouter which is not more likely to be killed by a fire as a juvenile (i.e. is not fire sensitive) the equation is:

$$t_1^* = \frac{A}{\lambda_p}$$

and for one which is sensitive to fire as a juvenile it is:

$$t_1^* = \frac{\ln\left(\frac{\lambda_s + \alpha\lambda_p}{\lambda_s + \lambda_p}\right)}{\lambda_p(\alpha - 1)}$$

6.2.4 Mortality rates

Data on the mortality rates of *Protea neriifolia* and *P. nitida* were taken from Haynes (1976) and Le Maitre (1992), and from Le Maitre & Midgley (1992) for *Orothamnus zeyheri*. The life tables were compiled for periodically monitored populations using the methods of Caughley (1978). Differences in mortality rates were assessed using the Logrank test (Hutchings *et al.* 1991). Clark (1991) argued that if the high mortality rates among seedlings and senescing adults were ignored, mortality during the remainder of the lifespan can be described by a negative exponential model. This simplification was used in this study as well.

6.2.5 Statistical analyses

The probability distributions were fitted to the data on fire recurrence intervals using maximum likelihood procedures. Some of the formulas had to be solved iteratively and the 'Optimiser Tool' in *Quattro™ Pro* version 6.1 was used to obtain a solution. The goodness of fit of the observed frequency distributions to frequency distributions calculated from the probability density functions for the different distributions was analysed using the Kolmogorov-Smirnov test (SAS 1985). This is conservative when used with discrete rather than continuous data (Daniel 1978).

6.2.6 Maximum likelihood methods for fitting probability distributions to data

Exponential: the maximum likelihood estimator for λ for the Exponential distribution is as follows (Johnson & Kotz 1970):

$$\hat{\lambda} = \frac{1}{\sum_{i=1}^{n} (\frac{t_i}{n})}$$

where n = the number of observations, and t_i = the duration (t) of time interval i.

Gamma: the distribution was fitted to the data using the procedure described by Lawless (1982, see also Johnson & Kotz 1970). This approach involves first calculating the arithmetic mean fire recurrence interval ($\hat{t}$) and the geometric mean fire interval ($\bar{t}$) from the data and then using the following maximum likelihood estimators:

$$\log(\hat{c}) - \psi(\hat{c}) = \log(\frac{\hat{t}}{\bar{t}})$$

$$\hat{c}\frac{1}{\hat{\lambda}} = \hat{t}$$

where ψ = the Digamma function. The first equation was solved for the parameter c ($\hat{c}$) by iteration. The Digamma function was estimated using the first five terms in a series approximation given in Lawless (1982):

$$\psi(x) = \ln(x) - \frac{1}{2x} - \frac{1}{12x^2} + \frac{1}{120x^4} - \frac{1}{252x^6}$$

Lawless (1982) also provides equations which can be used to estimate c directly from the data. These equations gave values which were very similar to those estimated by the maximum likelihood method.

Weibull: this distribution was fitted to the data using the approach described by Cohen (1965) and used by Johnson & van Wagner (1985) and Clark (1991). The maximum likelihood estimators are:

$$\frac{\sum_{i=1}^{n} t_i^c \ln t_i}{\sum_{i=1}^{n} t_i^c} - \frac{1}{c} = \frac{1}{n}\sum_{i=1}^{n} \ln t_i$$

$$\hat{\theta} = \sum_{i=1}^{n} \frac{t_i^c}{n} \quad \textit{where} \quad \theta = \frac{1}{\lambda^c}$$

where t_i = the fire recurrence intervals and n = the number of observations. This equation is solved

iteratively to provide an estimate for the parameter c ($\hat{c}$). The Gamma function values were calculated using the first five terms of the following series (Lawless 1982) as an approximation:

$$\ln\Gamma(x) = (x-\frac{1}{2})\ln(x) - x - \frac{1}{2}\ln(2\pi) + \frac{1}{12x} - \frac{1}{360x^3} + \frac{1}{1260x^5} - \ldots.$$

6.3 Results

6.3.1 Fire frequency distributions

The fire frequency distributions vary markedly between the five areas included in this study (Figure 6.1) with the Kammanassie having the shortest mean intervals and Kogelberg the longest (Table 6.1). The probability of a fire increases most rapidly with age in the Kammanassie where the greatest observed period between fires was 16 years. In the Cederberg the probability of a fire initially increased at a similar rate but the rate then decreased and the longest interval between fires was 30 years. Overall, the longest intervals were observed in the Kogelberg State Forest where the mean interval was 20 years, followed by Swartboskloof with 19. The slowest initial increase was observed in Swartboskloof where a large proportion of this relatively small area burnt between the ages of 13 and 16 years. These differences also can be seen in the values of the parameters for the different distributions (Table 6.2). The greater the value of c for both the Gamma and Weibull distributions the more the hazard of burning increases with time since the last fire. When c = 1 both distributions reduce to the Exponential distribution which has a constant probability of disturbance.

Table 6.1. Mean fire recurrence intervals (± standard error of the mean) for different areas in the mountain fynbos. These are derived from fitting the Exponential and Weibull distributions to data on fire return intervals using formulas for the mean and variance of the intervals given by Johnson & Kotz (1970) and Lawless (1982). For more information see the text.

Area	Exponential	Gamma	Weibull
Cederberg	14.08±1.41	14.08±091	14.22±1.65
Table Mountain	13.81±1.38	13.81±0.73	13.70±1.48
Swartboskloof	19.02±1.90	19.02±0.64	19.15±2.04
Kogelberg	20.00±2.00	20.00±1.64	21.67±2.48
Kammanassie	10.43±1.04	10.43±0.60	10.36±1.14
Desired	14.42±1.44	14.42±0.30	14.42±1.48

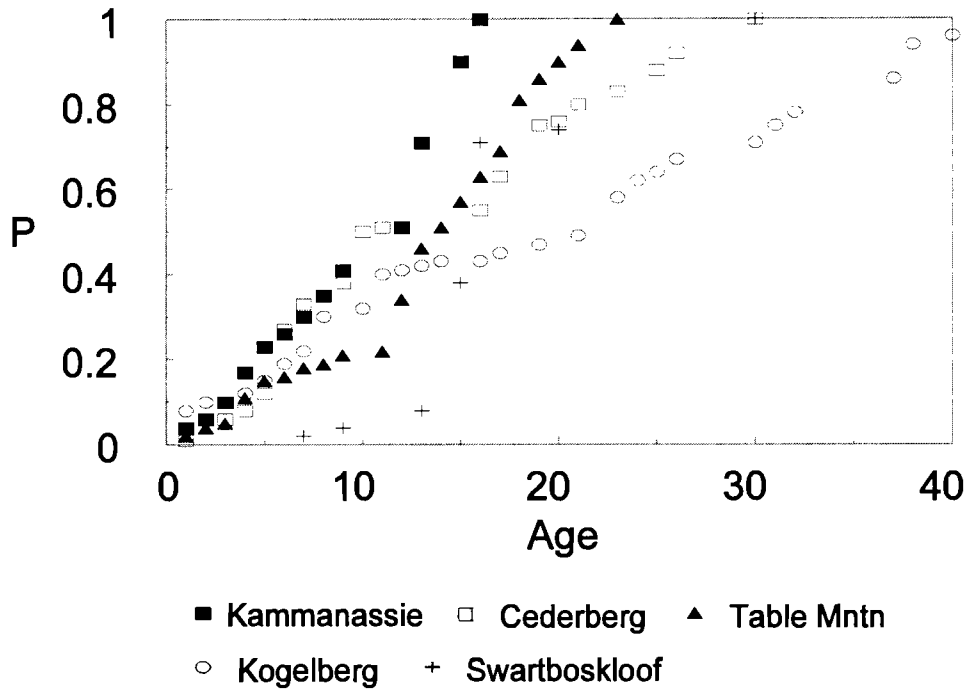

Figure 6.1 Cumulative probability (P) of a fire based on observed intervals between fires in five areas in the Western Cape. See the text for more information.

Table 6.2. Fitted parameter values for the Exponential, Gamma and Weibull distributions for the different areas. See Methods for more information on the maximum likelihood methods used to derive the parameter values.

Area	Parameter	Exponential	Gamma	Weibull
Cederberg	λ	0.0710	0.1688	0.0625
	c	-	2.2764	1.7693
Table Mountain	λ	0.0724	0.2579	0.0648
	c	-	3.5626	2.6167
Swartboskloof	λ	0.0526	0.4581	0.0466
	c	-	8.7315	2.9952
Kogelberg	λ	0.0495	0.0741	0.0455
	c	-	1.4825	1.3940
Kammanassie	λ	0.0959	0.2927	0.0855
	c	-	3.0532	2.3535
Desired	λ	0.0693	1.6231	0.0639
	c	-	23.4055	5.3125

The fitted models varied in the accuracy with which they were able to match the observed frequency distributions. The Kolmogorov-Smirnov test showed that the differences between the observed and predicted frequencies were significant with the following exceptions: (a) Cederberg and Desired (i.e. the hypothesised ideal distribution) for both the Gamma and Weibull distributions and (b) Table Mountain for the Weibull distribution. At the one extreme were areas such as the Kogelberg and Cederberg (Figure 6.2) with a slow, steady increase in the cumulative probability of a fire (Figure 6.1). In these cases all the distributions were similar because the probability of a fire was relatively similar in each time interval. However, even in this case it is evident that the Exponential distribution overestimates the risk of a fire at a young age and underestimates it at older ages. At the other extreme were sites such as Swartboskloof (Figure 6.3) with rapid increase in the cumulative probability of fire from 10 to 25 years after fire. In this case the assumption in the Exponential distribution of a constant probability of a fire clearly does not apply. The Gamma distribution provides the best fit but the predicted values differ very little from the Weibull distribution. The hazard-of-burning function for the Weibull distribution increased with time since fire at all sites, showing that the probability of a fire definitely increases with time after fire (see Figure 6.4 for the Cederberg as an example where c = 1.77). The lack of a marked concentration in the annual

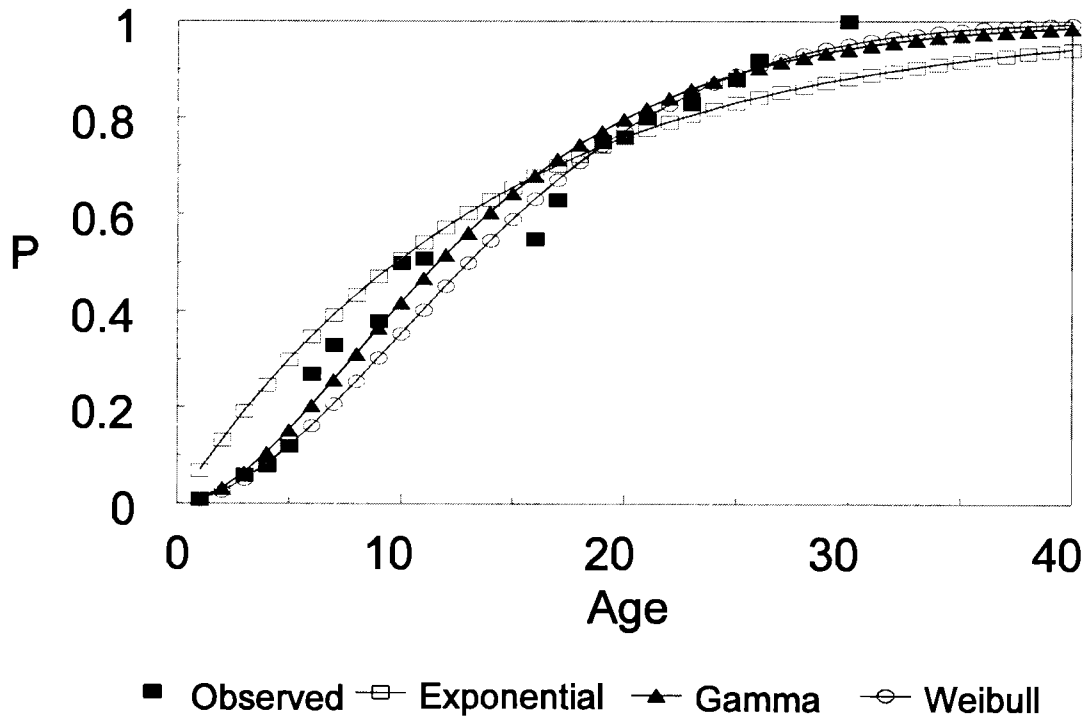

Figure 6.2 Observed and fitted cumulative probability (P) distributions for the Cederberg area. For more information on the fitting of the different distributions see Methods.

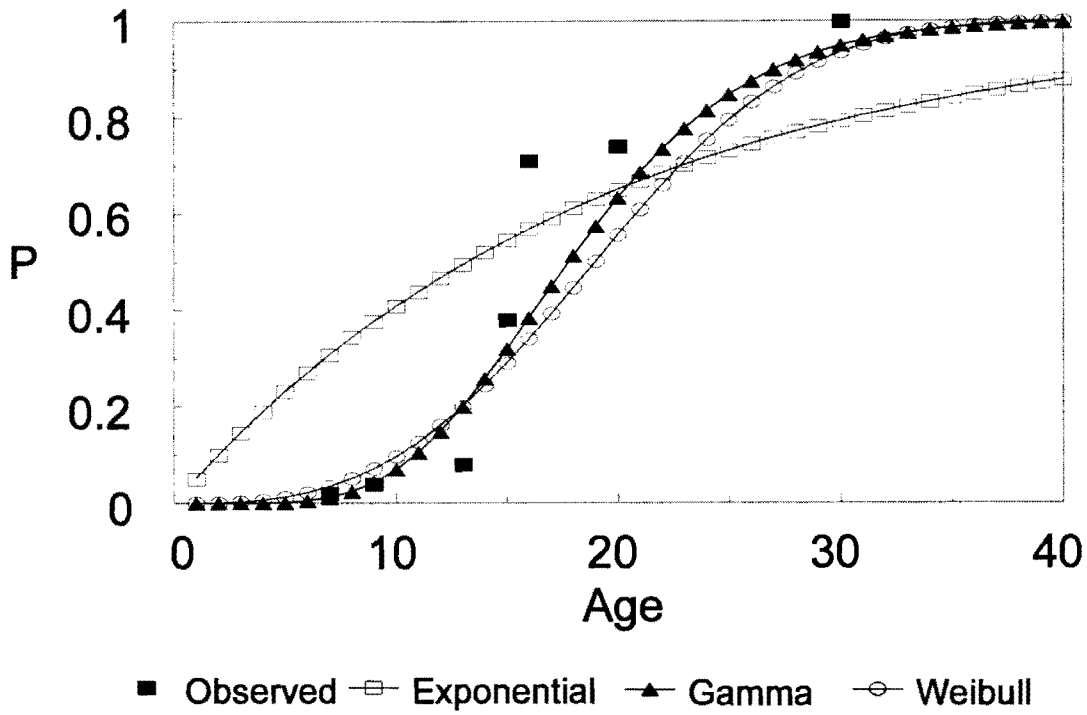

Figure 6.3 Observed and fitted cumulative probability (P) distributions for fires for Swartboskloof. For more information on the fitting of the distributions see Methods.

probability of a fire between certain ages is clearly visible in the shallow curve of the probability density function (Figure 6.4).

6.3.2 Age at first reproduction

Protea neriifolia produced its first inflorescences at a post-fire age of four years (Table 6.3). The seeds require several months to mature so the plants would not be able to regenerate after fire until late in their fourth year from germination. *Protea nitida* requires substantially longer to reach flowering with a minimum of eight years under good conditions (Table 6.3). Even during long intervals without fires maturation was slow with a small proportion of new recruits maturing (Table 6.4). No plants in size class 'i', typically ones that have survived a fire, matured during this period.

Reproductive maturation of *Orothamnus zeyheri,* a non-serotinous species was similar to serotinous proteas. The first plants came into flower at five years of age and it took about nine years for half of a population to have flowered at least once. This was contrary to the prediction that its juvenile period should be shorter than those of serotinous species given the same fire frequency distribution.

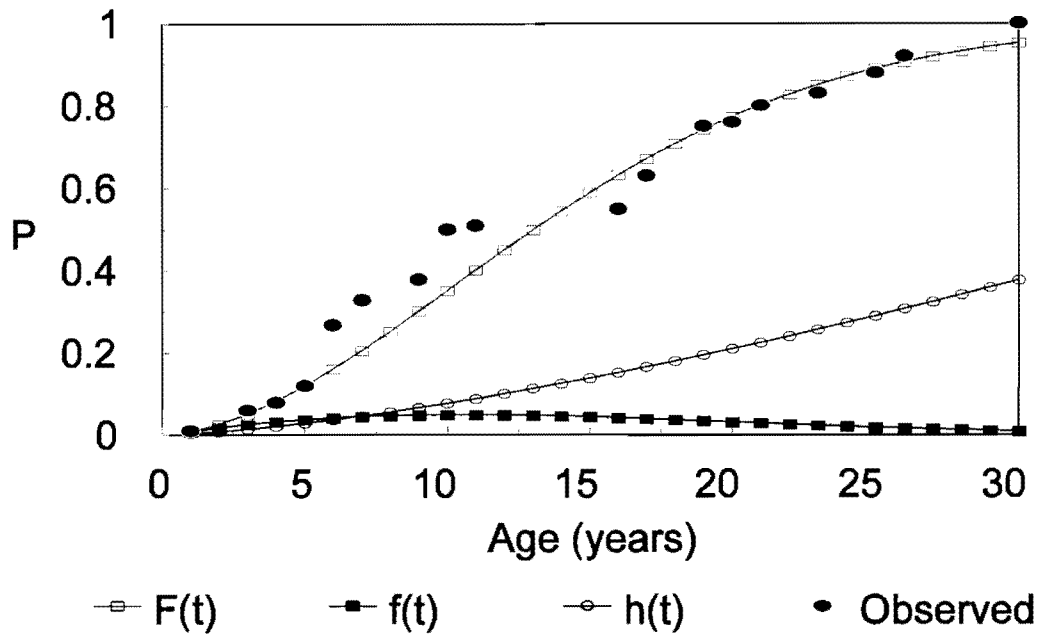

Figure 6.4 Cederberg fire data showing the observed cumulative probability (P) of a fire and the fitted Weibull cumulative probability distribution {F(t)}, probability density function {f(t)} and hazard function {h(t)} based on formulas provided by Clark (1991). For more information on distribution fitting see Methods.

Table 6.3 Age at first reproduction for the three Proteaceae included in this study. The number in parentheses is the age by which at least 50% of the population had, or is estimated to have, flowered at least once.

Species	Site	Age at first reproduction (years)	Source
Protea neriifolia	Jonkershoek	4 (8)	Le Maitre (1992)
	Jakkalsrivier	4 (6)	Chapter 2
Protea nitida	Jonkershoek	8 (15-30)	Le Maitre (1992) & pers. obs.
Orothamus zeyheri	Kogelberg	5 (9)	Boucher (1981) & Le Maitre *et al.* (1991)

6.3.3 Mortality rates and lifespans

Mean annual mortality rates of *Protea neriifolia* initially declined with age and then increased again in older plants (Figure 6.5). Overall the mortality rates were lowest for young plants at Jakkalsrivier (0-10% per year) but somewhat higher for the older plants at Swartboskloof (1-12%) and Langrivier (1-22% Table 6.5). Mortality rates varied widely between observations within populations with the highest rates being for 30-34 year old plants at Langrivier. Mortality rates were significantly different between the Swartboskloof and Langrivier populations (Logrank test = 289.06, Chi-square$_{1\ DF}$ P<0.01). Mortality during the first year and after 30 years of age is quite high. The mean annual mortality rate during the period from 1-30 years of age was about 5.6% per annum.

Table 6.4 Maturation of different populations of *Protea nitida* during long periods without fires or with only a single fire (after Le Maitre 1992). The different size classes are as follows: new = new individuals recruited as seedlings; i = short plants with a single dominant shoot; ii = multi-stemmed plant with juvenile form; iii = plants with a single stem and mature, rounded canopy <2.5 m tall; iv = like iii but >2.5 m tall (Haynes 1976; Le Maitre 1992).

Fire	None		None		One	
Period (years)	12.28		10.77		10.7	
Size class	No.	Proportion	No.	Proportion	No.	Proportion
New	38	0.03	42	0.00	71	0.01
i	8	0.00	56	0.00	128	0.00
iij	46	0.21	104	0.08	89	0.25
iiij	16	0.57	32	0.47	4	0.25

Mortality rates of *Protea nitida* decreased with increasing size and maturity (Table 6.6). The ages of the plants in the different size classes are not known but plants in classes iii and iv are probably at least 20 years old and possibly far older. During periods without fires there was no mortality of plants in size class iv compared 25-83% of class i and 11-25% of immature class ii plants. The same pattern of a high mortality of plants in the small size classes occurs during fires except at high intensity when nearly 30% of mature class iii and 10% of class iv plants died. Annual mortality rates ranged from 0.02-0.07 for class i plants between fires and 0.2-0.6 following fires compared with 0.00-0.01 and 0.00-0.10, respectively, for class iv plants. The nature of the data makes it very difficult to estimate the annual mortality rates during the majority of the lifespan. If a constant mortality rate is assumed

Table 6.5 Lifetable for *Protea neriifolia* based on data from monitoring plots at three sites. Jakkalsrivier is situated about 30 km south-east and in a similar environment to the other sites which are both located in the Jonkershoek Valley near Stellenbosch. lx = the proportion surviving; dx = the proportion dying during the period of time from x-1 to x; qx = the proportion alive at age x-1 which died before time x; dx (per year) = the mortality expressed on an annual basis.

Jakkalsrivier - germination winter 1980					
Age (years)	No. alive	lx	dx	qx	dx (per year)
0.91	99	1.0000			
1.45	99	1.0000	0.0000	0.0000	0.0000
2.04	93	0.9394	0.0606	0.0606	0.1027
2.86	92	0.9293	0.0101	0.0108	0.0123
4.02	88	0.8889	0.0404	0.0435	0.0348
5.18	87	0.8788	0.0101	0.0114	0.0087
7.82	87	0.8788	0.0000	0.0000	0.0000
8.83	87	0.8788	0.0000	0.0000	0.0000
9.69	86	0.8687	0.0101	0.0115	0.0117
Swartboskloof - germination winter 1958					
Age (years)	No. alive	lx	dx	qx	dx (per year)
14.94	1157	1.0000			
16.58	1000	0.8643	0.1357	0.1357	0.0823
17.56	870	0.7519	0.1124	0.1300	0.1146
19.06	824	0.7122	0.0398	0.0529	0.0265
20.42	642	0.5549	0.1573	0.2209	0.1156
22.26	618	0.5341	0.0207	0.0374	0.0113
24.35	546	0.4719	0.0622	0.1165	0.0298
28.64	331	0.2861	0.1858	0.3938	0.0433
Langrivier - germination winter 1942					
Age (years)	No. alive	lx	dx	qx	dx/year
30.71	215	1.0000			
32.60	129	0.6000	0.4000	0.4000	0.2117
33.46	89	0.4140	0.1860	0.3101	0.2157
35.04	61	0.2837	0.1302	0.3146	0.0824
36.42	38	0.1767	0.1070	0.3770	0.0775
38.19	34	0.1581	0.0186	0.1053	0.0105
40.41	22	0.1023	0.0558	0.3529	0.0251
45.36	7	0.0326	0.0698	0.6818	0.0141

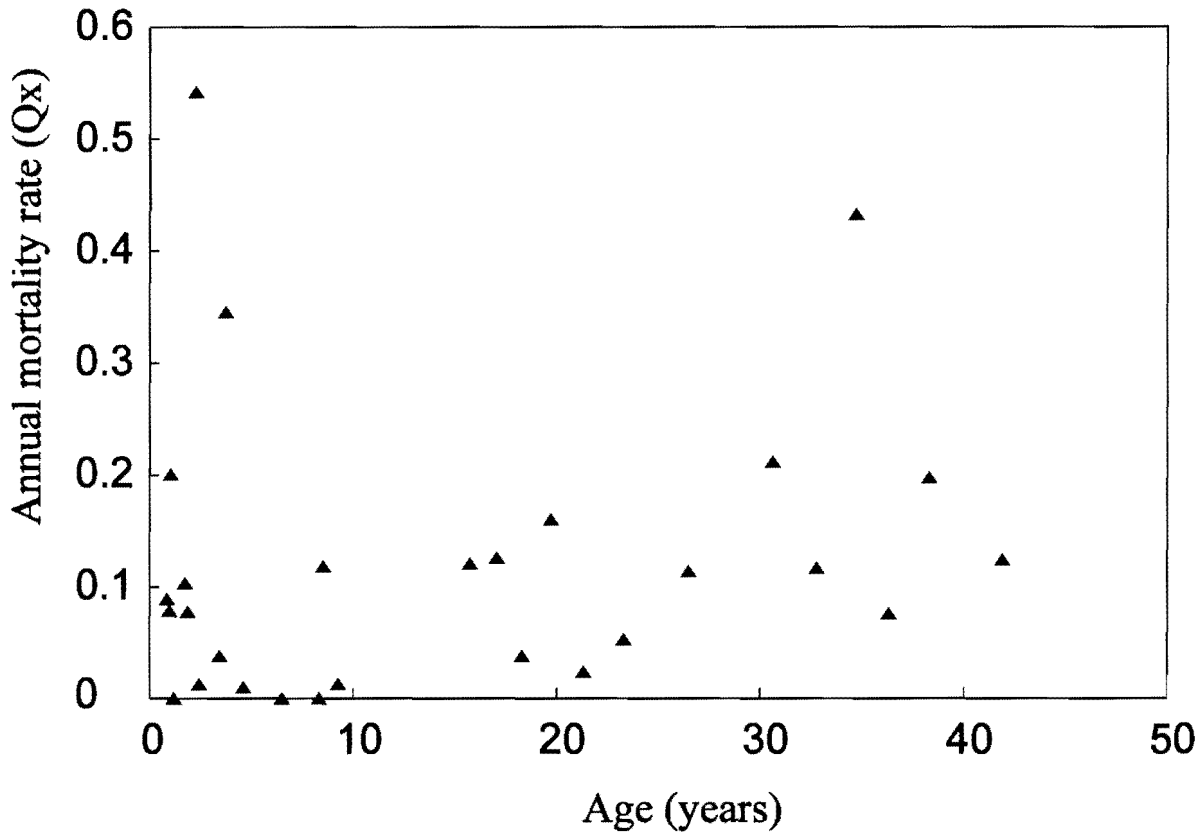

Figure 6.5 Annual mortality rate of monitored *Protea neriifolia* populations at different ages. Data combined from three different sites (after Le Maitre 1992, see also Table 6.5).

Table 6.6 The proportion of *Protea nitida* plants in different size classes in monitored populations which died between and following fires of different intensities (after Le Maitre 1992). Size classes are described in the caption of Table 6.4.

Fire occurrence / intensity	None	None	One	Low	Moderate	High
Period since fire	12.28	10.77	10.7			
Size class						
New	0.00 (38)	0.05 (42)	0.18 (71)	0.00 (67)	0.00 (1038)	0.00 (354)
i	0.25 (8)	0.80 (56)	0.83 (128)	0.33 (6)	0.50 (16)	0.65 (16)
iij	0.11 (46)	0.18 (104)	0.25 (89)	0.13 (116)	0.14 (103)	0.32 (41)
iia	0.00 (2)	0.05 (22)	0.06 (33)	0.00 (24)	0.00 (5)	0.37 (19)
iiij	0.06 (16)	0.06 (32)	0.00 (4)	0.00 (6)	0.08 (24)	0.00 (2)
iiia	0.02 (123)	0.03 (32)	0.03 (61)	0.00 (68)	0.06 (49)	0.29 (99)
iva	0.00 (15)	0.00 (22)	0.07 (30)	0.00 (48)	0.14 (43)	0.10 (40)

then the mean annual mortality rates over long periods of time (Table 6.6) for the different size classes were: class i = 12.0 %, iij = 2.0% and iia-iv = 0.4%. The last rate best represents the mortality rate over most of the lifespan and is used in the estimation of juvenile periods.

Table 6.7 Lifetable for *Orothamnus zeyheri* based on data from monitoring plots at three sites situated in the Kogelberg State Forest (after Le Maitre *et al.* 1991 and unpublished data). For an explanation of the abbreviations see Table 6.4.

Site 10					
Age (yrs)	No. alive	lx	dx	qx	dx (per year)
0.97	88	1.0000			
3.44	88	1.0000	0.0000	0.0000	0.0000
4.12	86	0.9773	0.0227	0.0227	0.0333
4.70	67	0.7614	0.2159	0.2209	0.3720
5.41	65	0.7386	0.0227	0.0299	0.0321
5.93	58	0.6591	0.0795	0.1077	0.1537
7.94	54	0.6136	0.0455	0.0690	0.0226
10.58	33	0.3750	0.2386	0.3889	0.0903
Site 15					
Age (yrs)	No. alive	lx	dx	qx	dx (per year)
1.00	450	1.0000			
6.00	300	0.6667	0.3333	0.3333	0.0666
15.00	75	0.1667	0.5000	0.7500	0.0556
17.08	17	0.0378	0.1289	0.7733	0.0619
20.33	7	0.0156	0.0222	0.5882	0.0068
21.67	5	0.0111	0.0044	0.2857	0.0033
Site 17					
Age (yrs)	No. alive	lx	dx	qx	dx (per year)
0.75	214	1.0000			
1.33	177	0.8271	0.1729	0.1729	0.2951
1.61	159	0.7430	0.0841	0.1017	0.3012
2.75	110	0.5140	0.2290	0.3082	0.2020
3.00	75	0.3505	0.1636	0.3182	0.6495
4.60	60	0.2804	0.0701	0.2000	0.0437
7.58	34	0.1589	0.1215	0.4333	0.0408

Mortality rates also varied among populations of *Orothamnus zeyheri* and within populations there were marked fluctuations between years (Table 6.7). The highest mortality rates were recorded in population 15, particularly from 2.0 to 3.0 years of age. The mean annual mortality rate from 1-20

years of age for these populations was about 14.8% per year. This is much higher than was recorded for the serotinous *P. neriifolia* and supports the prediction that the mortality rates would be higher in species with long-lived seeds.

The lifespan of *P. neriifolia* appears to be about 45 years at the Langrivier site (Table 6.5) compared with less than 25 years for *O. zeyheri* (Table 6.7). This supports the hypothesis that species with seeds that are short-lived after the death of the parent should have longer lifespans than species with long-lived seeds. No data are available on the lifespan of *P. nitida* but the low mean mortality rate of 0.04% in mature plants suggests a long lifespan. If the assumption that mortality rates are constant over most of the lifespan (i.e. follow an exponential distribution) is correct, the half-lives of the species can be calculated from the mean mortality rates. This gives values of 4.68 years for *O. zeyheri*, 12.38 years for *P. neriifolia* and 173.28 years for mature *P. nitida*.

6.3.4 Optimal juvenile periods

An unfortunate consequence of the mathematical constraints inherent in renewal theory is that optimal juvenile (pre-reproductive) periods could only be determined for seeders for the Exponential and Gamma distributions, while only the former can be used for sprouters. This means that optimal sprouter juvenile periods can only be predicted for a constant probability of fire.

The predicted optimal juvenile periods for seeders varied between sites with the longest juvenile periods being predicted for Swartboskloof and the shortest for the Kogelberg (Table 6.8). This was because the length of the juvenile period was strongly influenced by the rate at which the probability of a fire increased in the first few years after a fire. In the Kogelberg the probability of a fire was high initially (Figure 6.1) while for Swartboskloof the probability was initially low (Figures 1 & 3). The assumption of a constant probability of a fire (exponential distribution) also resulted in the prediction of very short juvenile periods compared with those based on the Gamma distribution which were closer to those observed (Table 6.3). The higher mean annual mortality rate of *O. zeyheri* resulted in it having shorter juvenile periods than those predicted for *P. neriifolia*, supporting the hypothesis, but contrary to records based on field surveys (Table 6.3). The difference between the predictions from the Exponential and Gamma distributions also increased as the predicted optimal juvenile period increased. The predicted optimal juvenile period (assuming constant fire probabilites) for *Protea nitida*, a sprouter which is fire-sensitive when young, was not out of the observed range but was shorter than the mean time estimated from field studies. It was not possible to estimate the juvenile

period for *P. nitida* for the Gamma distribution, but judging by the differences predicted for seeders, they would undoubtedly have been substantially longer.

6.3.5 Sensitivity of the models to parameter values

The parameter values for the mortality rate and the parameter α (which is the reciprocal of the ratio of the juvenile period to the lifespan) were somewhat uncertain because the data from observations of fynbos Proteaceae are limited or lacking. This section examines the effects of varying the magnitude of the values of these parameters over a representative range of values.

The effect of changing the mean annual mortality rate on the predicted juvenile period differed between seeders and sprouters (Figure 6.6). The exact values varied between sites as they did in Table 6.8 but the patterns remained the same. As the mortality rate increased from zero the predictions for seeders from the Exponential and Gamma distributions diverged. The juvenile period

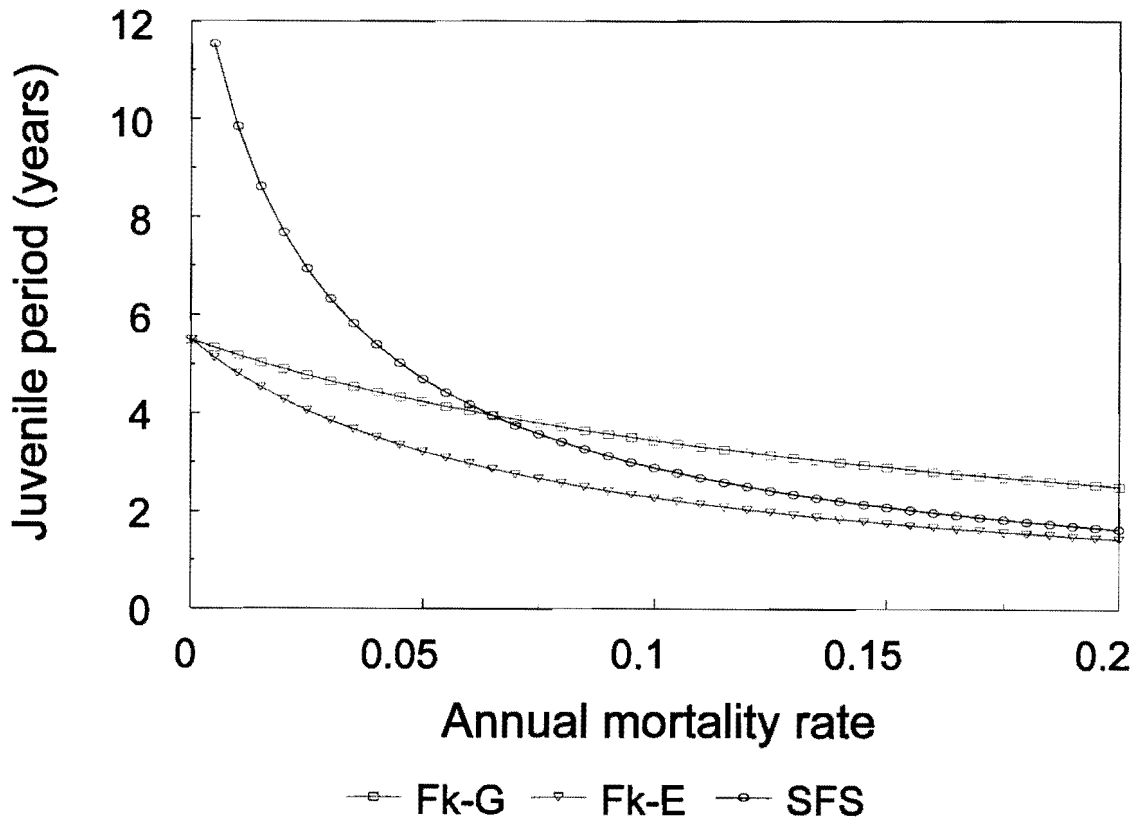

Figure 6.6 The relationship between the mean annual mortality rate and the predicted length of the juvenile period for a seeder using the Gamma distribution (Fk-G) and the Exponential distribution (Fk-E), and a fire-sensitive sprouter (SFS). Data for the other parameters of the models were taken from the Cederberg data (Table 6.8).

predicted by the Gamma distribution was less sensitive to the mean annual mortality rate than those based on the Exponential distribution. The predictions for the fire-sensitive sprouter tended to infinity as the mortality rate neared zero and became shorter than those predicted for a seeder when the mortality rate was greater than about 0.06. This may have had a marked impact on the estimates of the juvenile period for these species because the mortality rates were typically very low or negligible for mature plants (Table 6.7). The similar length of the juvenile period of *P. neriifolia* and *O. zeyheri* was consistent with the predictions of the juvenile period from the Gamma distribution (Figure 6.6). Although mortality rates differed approximately 3-fold (0.056 versus 0.148 respectively) the difference in the predicted juvenile period was only about two years.

The value for the parameter α of 5.4, and thus a value for A of 0.39 (see Methods), was taken from the literature and not based on observations on local species. The value for α is the inverse of the ratio of the juvenile period to the lifespan of the plant. The predicted optimal juvenile periods for a

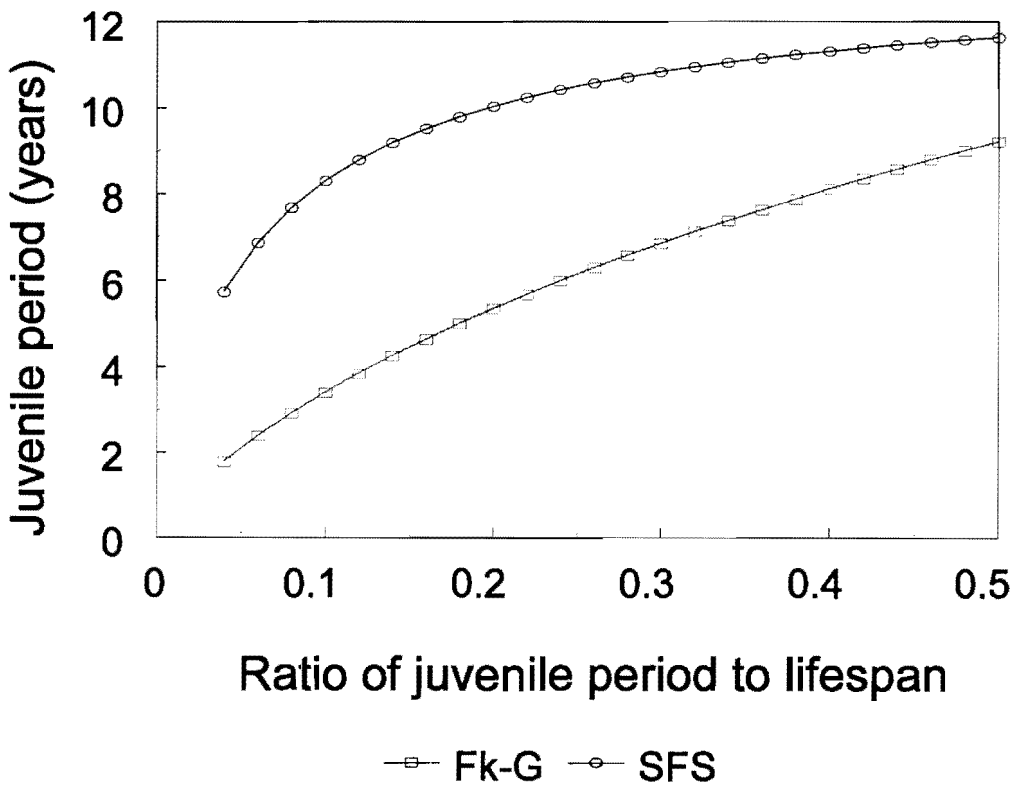

Figure 6.7 The relationship between the ratio of the juvenile period to the lifespan and the predicted juvenile periods for a seeder (Fk-G) based on the Gamma distribution and a fire-sensitive sprouter (SFS). The values for the parameters λ and c were taken from the Cederberg data (Table 6.8) and the mean annual mortality rate was set at 0.056 for the seeder and 0.004 for the sprouter.

seeder and fire-sensitive sprouter were calculated for a representative range of values of the ratio of the juvenile period to the lifespan (Figure 6.7). The length of the optimal juvenile period increased as the ratio of the juvenile period to the lifespan increased. The predictions for the fire-sensitive sprouting species increased more rapidly at low ratios because this equation used the parameter α while the equation for the seeder used A which was less sensitive to changes in the ratio. If, for example, the lifespan of *O. zeyheri* was about 25 years, its juvenile period was five years, and its mean annual mortality rate (r) was 0.148, then α would be 5 and A = 0.40 and the predicted juvenile period would be 3.02 years, little different to that predicted earlier (Table 6.8). For *P. neriifolia* with a lifespan of 45 years, juvenile period of 4 years and mean annual mortality rate of 0.056 it would have been 2.50 years which was much less than the predicted 4.12 years (Table 6.8). If the corresponding values for *P. nitida* were 150, 20 and 0.004, then the juvenile period was 11.44 years which is very similar to the predicted values (Table 6.8).

Table 6.8 Actual and predicted optimal juvenile periods for *Orothamnus zeyheri, Protea neriifolia* (both species killed by fire), and *P. nitida* a sprouting species which is fire sensitive as a small (juvenile) plant. For more detail on the actual data see Table 6.3. Estimates were calculated using formulas provided by Clark (1991). The values of the parameters are given in Table 6.2 and the mean annual mortality rates were: *O. zeyheri* = 0.148, *P. neriifolia* = 0.056 and *P. nitida* = 0.004. Values in bold are for sites where the species was studied. See the text for more information.

Site	Probability distribution	Seeder (years)		Sprouter (years)
		O. zeyheri	*P. neriifolia*	*P. nitida*
Actual		5	4	15-30
Cederberg	Exponential	1.75	3.07	12.01
	Gamma	2.93	4.12	-
Table Mountain	Exponential	1.76	3.04	11.82
	Gamma	3.42	4.43	-
Swartboskloof	Exponential	1.94	**3.59**	**15.45**
	Gamma	5.61	**6.61**	-
Kogelberg	Exponential	**1.97**	3.68	16.10
	Gamma	**2.60**	4.44	-
Kammanassie	Exponential	1.59	2.57	9.25
	Gamma	2.70	3.41	-
Desired	Exponential	1.79	3.11	12.26
	Gamma	5.15	5.44	-

This analysis suggests that, unless the values for the parameters derived from the data sets used in this study are seriously in error, the estimated juvenile period and lifespan is most critical for seeders with low mortality rates.

6.4 Discussion

6.4.1 Fire frequencies

The fire frequency distributions varied between the different study areas (Figure 6.1) although the mean fire frequencies varied relatively little (Table 6.1). The extent to which these regimes represent those that prevailed in the past is uncertain. Hominids inhabiting the Cape region have deliberately used fire for at least 1-1.5 million years (Deacon 1992). In most areas fire suppression by humans has only been effective this century but patch burning to enhance the quality of the veld for grazing has remained a common practice despite attempts to regulate it. Overall, different factors may have resulted in increases and decreases in fire frequencies but the continued existence of fire-frequency-sensitive Proteaceae in these areas suggests that recent fire-frequencies have been within the range that the species have adapted to survive.

The Cederberg Mountains are situated in the north-western region of the fynbos and have a strongly Mediterranean climate with 80% of the rainfall occurring in winter (Brown *et al.* 1991). The summers are hot and dry, most of the fires occur in summer and the mean interval was given as 11-15 years compared with the 14 years estimated in this analysis (Table 6.1). About half the fires are of natural origin, ignited mainly by lightning, and anthropogenic fires comprise about 24% of all fires. Fires were actively suppressed until policy changed in 1973 and this would have resulted in longer intervals between fires than under pre-colonial conditions. Table Mountain, Swartboskloof and the Kogelberg area are situated in the south-west with a greater proportion of rainfall (30% plus) in summer (Van Wilgen & McDonald 1992; Richardson *et al.* 1994). These mountain areas have a higher risk of anthropogenic fires than the Cederberg as the adjacent lowlands are densely inhabited. Fire frequencies in all these areas, particularly the Kogelberg, were also influenced by a history of deliberate fire suppression and active fire protection using an extensive network of firebreaks.

The Kammanassie Mountains are situated inland in the southern region of the fynbos with a bimodal rainfall with peaks in summer and winter. All the fires in the database for this remote area were of

natural origin and most were caused by lightning. The fire regime is similar to that of the Swartberg with the main fire season being late summer (Horne 1981). The observed fire regimes at the different sites, except the Kammanassie, all have been influenced by human activities and therefore may differ from those under natural conditions.

No comparable analyses of fire frequency data could be found for areas in the seeder dominated Mediterranean shrublands of Australia or California. Studies of the seed banks and demography of seeding Proteaceae in the ecologically similar kwongan and heath vegetation in Australia (Le Maitre & Midgley 1992, Cowling *et al.* 1994) suggest that fire frequencies were similar with a desired mean interval of about 15 years and a range of about 10-25 years (Bradstock & Myerscough 1988, Bradstock & O'Connell 1988, Bradstock 1990, Cowling *et al.* 1990, Enright *et al.* 1996).

6.4.2 Age at first reproduction

There is a general lack of reliable data on juvenile periods and especially on the lifespans of Cape Proteaceae. The juvenile periods recorded in this study are within the range for fynbos of 4-7 years for a number of species in the Proteaceae (Williams 1972, Moll *et al.* 1980, Rourke 1980, Kruger & Bigalke 1994). Data from the Kogelberg show that juvenile period ranges from as short as three years (*Leucadendron microcephalum, Diastella fraterna, Leucospermum truncatulum*) to 7-8 years (*Leucadendron laureolum, Mimetes hottentoticus*) or nine years (*Mimetes arboreus*) (Le Maitre *et al.* 1991). Records of the juvenile periods for seeders in the ecologically very similar genus *Banksia* show that they range from three to six years, rarely more (Bradstock & Myerscough 1981, Cowling *et al.* 1987, Bradstock & O'Connell 1988, Lamont *et al.* 1991a, Burgman & Lamont 1992). There was no evidence that the juvenile period of *O. zeyheri* was any shorter that of *Protea neriifolia* (Table 6.3) contrary to the predictions of a difference between species with long and short-lived seeds. On the other hand the serotinous *Protea stokoei* occurs in similar montane habitats to *O. zeyheri* and it has a juvenile period of about 8-11 years (Le Maitre *et al.* 1991).

No other data sets for fynbos could be found to compare with the data for a sprouting species like *Protea nitida* which requires a minimum of eight and typically of the order of 15-30 years to mature (Table 6.3). The primary juvenile periods (seedling to seed production) for tall, sprouting, kwongan Proteaceae were similar. For *Banksia serrata* it was >23 years and for *Isopogon anemonifolius* about

20 years (Bradstock 1990). Maturation could also be delayed by fires during this period; a 15 year fire cycle could extend the juvenile period to 30 and 21 years respectively. For *B. tricuspis* the primary juvenile period was >20 years (Lamont & van Leeuwen 1988), *B. grandis* 25-35 years (Abbott 1985) and *B. oblongifolia* >23 years (Zammit & Westoby 1987b).

6.4.3 Mortality rates and lifespans

The monitoring plots in Swartboskloof , Langrivier and Jakkalsrivier (Table 6.5, Chapter 2) are the only source of reliable data on senescence and lifespans in old stands of tall, serotinous, Proteaceae shrubs although estimates ranging from 25-50 years were given by Moll *et al.* (1980). A fire burnt the Langrivier monitoring plot in October 1987 so data on maximum longevity for *Protea neriifolia* are lacking but it was probably not much more than the observed 45 years as the remaining mature plants were nearly dead (Le Maitre pers. obs.). The data for Langrivier suggest that mortality rates for *Protea neriifolia* are high but relatively constant from about 30-45 years (Table 6.5) and thus lack the marked increase typical of senescence. There was little or no mortality and no sign of senescence in *P. neriifolia* stands of the same age and on similar soils but about 300 m higher in the Langrivier catchment (D. Le Maitre pers. obs.), suggesting that growth rates and lifespans are inversely correlated, which supports Loehle's (1988) hypothesis. The ages of senescence of populations of similar seeders in the Australian genus *Banksia* range from about 30-50 years with maximum lifespans of about 45-50 years (Bradstock & Myerscough 1981, Gill & McMahon 1986, Cowling *et al.* 1987, Bradstock & O'Connell 1988, Lamont *et al.* 1991a, Burgman & Lamont 1992).

In this study the mean annual mortality rate of *Protea neriifolia* during the majority of its reproductive lifespan was about 0.056. Mortality rates for similar serotinous species ranged from 0.047 for *Leucadendron laureolum* to 0.070 for *Aulax umbellata* (Le Maitre *et al.* 1991). Mortality rates of 0.030-0.037 were observed for stands of *Protea lacticolor* (1-10 years old) and 0.074 for 22-31 year old plants (Chapter 2). The corresponding mortality rates for *Leucadendron xanthoconus* at the same site were 0.061 and 0.090 respectively. Similar mean annual mortality rates of 0.01-0.13 during the majority of the lifespan have been recorded for seed-regenerating, serotinous, Australian Proteaceae (Bradstock & O'Connell 1988; Morris & Myerscough 1988; Witkowski *et al.* 1991).

The mean annual mortality rate for populations of *Orothamnus zeyheri* was 0.148 (Table 6.7). This was substantially higher than the mortality rates of *P. neriifolia* (Table 6.5), supporting the

hypothesis that species with long-lived seeds would have higher mortality rates. There was also no evidence of an increase in mortality rates, i.e. senescence, in old *O. zeyheri* populations (see also Boucher 1981). The maximum lifespan of *O. zeyheri* is probably less than 25 years, which is substantially less than the 35+ years of *P. neriifolia*. The *O. zeyheri* populations at sites 10 and 15 were protected from interference, for example through flower harvesting, unlike population 15 which was visited by flower harvesters (Boucher 1981, Le Maitre *et al.* 1991). The extent to which this affected the mortality rates at site 15 is not known but they are not particularly high compared with the other populations. Herbivory and topping of seedlings (at least 36% of plants) was also recorded in *O. zeyheri* populations and may account, in part, for the high mortality rates at site 17 (Boucher 1980). The only comparable mortality rate was 0.283 for the ecologically similar *Mimetes hottentoticus*, but other relatively short-lived species such as *Serruria elongata* and *Leucospermum truncatulum* had mortality rates of 0.063 and 0.048, respectively (Le Maitre *et al.* 1991).

The maximum lifespan of *O. zeyheri* is not accurately known. Many new populations were located when they regenerated from seeds following fires in vegetation which was last burnt some 22-24 years before (Boucher 1980, 1981). No living adults were found at these sites before the fires and at some other sites only a small number of senescent plants remained (e.g. site 15). These observation suggest that the lifespan is typically less than 25 years. *Acacia suaveolens* is an ant-dispersed, Australian heathland species with a juvenile period of 2-5 years, a lifespan of about 20 years (half-life 3.7 years) and a seed lifespan of at least 40 years (Auld 1987). Its mean annual mortality rate was about 0.19 which is within the range of those observed in *O. zeyheri* (Table 6.7).

Clark (1991) also suggested two approximations for the length of the juvenile period. For high mortality rates $t_1 \approx 0.4 \div$mortality rate. *Orothamnus zeyheri* had a high mean annual mortality rate of 0.148 which predicts that its juvenile period should be 2.70 years, about half the observed 5 years (Table 6.3). For low mortality rates the approximation is $t_1 \approx 0.4 \times$the expected (mean) fire interval. *Protea neriifolia* had comparatively low mortality rates (mean of 0.056) and the juvenile periods are predicted to range from 4.2 years (Kammanassie) to 8.0 years (Kogelberg) similar to both the observed (Table 6.3) and predicted juvenile periods based on the Gamma probability distributions (Table 6.8).

Sprouting Proteaceae are susceptible to fires when small, but *Protea nitida* seedlings and young plants are more resilient (Table 6.6) than some *Banksia* species and *Isopogon anemonifolius* where

complete mortality was observed in plants younger than 14-17 years of age (Bradstock & Myerscough 1988, Lamont & van Leeuwen 1988).

Data on the lifespans of sprouters like *Protea nitida* are very limited and primarily based on inference. Enright & Lamont (1992) estimated that *Banksia attenuata* could have a lifespan of 300 years. Studies of the lignotubers of *Eucalypt* species using carbon dating found that maximum ages were typically 190 years or less (Wellington *et al.* 1979, Head & Lacey 1988) but can reach 390-540 years where the non-living tissues are well preserved (Head & Lacey 1988). The lifespans could potentially be much longer but the death and decay of old lignotuber tissues results in a lack of positively datable remnants. Thus an absolute age can not be given but it is clear that sprouters can have lifespans on the order of hundreds of years.

The observed mean annual mortality rates of 0.008 for *Banksia serrata* and 0.005 for *Isopogon anemonifolius* (Bradstock & Myerscough 1988), both sprouting species, are close to the rate of 0.004 estimated for *P. nitida* in this study (Table 6.6). Mean annual mortality rates for a mallee eucalypt of 0.003 also are close to those of Proteaceae (Wellington & Noble 1985). If a relatively constant mortality rate holds true for the adult *P. nitida* plants, then the mean annual rate of 0.004 results in a half-life of 138 years. Some very large *P. nitida* individuals (8 m tall) still occur, and similar sized plants may have been widespread in the past but were harvested for their valuable firewood. This, together with the limited evidence from other species summarised above, suggests that a maximum lifespan of the order of 100 or more years is quite likely for this species.

6.4.4 Optimal juvenile periods

The optimal juvenile periods for seeding species that were predicted from the available fire data and for an increasing probability of fire with increasing post-fire age (Gamma distribution) were reasonably close to what has been observed in field studies (Table 6.3, Chapter 2). Those predicted for the Exponential distribution are clearly unrealistically short. This is due to the high probability of fire in young fynbos which is predicted by this distribution model because it assumes that the probability of a fire is constant. The same problem has also affected the estimates of the juvenile periods of *Protea nitida* which are shorter than expected but estimates using the Gamma distribution are not possible because the optimal juvenile period cannot be calculated for this distribution.

The predicted juvenile periods are quite sensitive to the value of the annual mortality rate, especially those of sprouting species with low mortality rates (Figure 6.6). The predictions for seeders for the Gamma distribution are the least sensitive to variations in the mortality rates given the range of mean annual mortality rates recorded for serotinous *Protea* and *Banksia* species of 0.05-0.15 (Bradstock & O'Connell 1988, Le Maitre *et al.* 1991, Witkowski *et al.* 1991, Chapter 2).

The predicted juvenile periods are also sensitive to the ratio of the juvenile period (t_1) to the lifespan (t_2) (Figure 6.7). Most of the predictions used in this paper were based on Loehle's (1988) fitted regression coefficient, $b = t_1/t_2$, of 0.187 for angiosperm trees and shrubs. A re-analysis of Loehle's (1988) data shows that the regression coefficient has a standard deviation of 0.095 which gives it a range of roughly 0.10-0.28. This range of variation has a marked effect on the value of α ($=1/b$) which can be seen in the sensitivity of the juvenile period of a fire-sensitive sprouting species (Figure 6.7). Juvenile periods of seeder species are less sensitive to the value of the regression coefficient because their optimal period depends on the value of A (see methods for the conversion of α to A) which is less sensitive to the changes in the regression coefficient. The regression coefficient for Loehle's (1988) data for shrubs is 0.195±0.019 (R-squared = 0.91, n = 12, α = 5.12) and for trees 0.162±0.021 (R-squared = 0.59, n = 41, α = 6.17). These differences imply that shrub species have delayed maturation relative to their lifespans when compared with trees. Quite why this is so is uncertain but the shrub lifespans were shorter than those of trees, 51 versus 173 years. The value for shrub species was much closer to the value used for the analyses in this study than was the value for tree species. The estimated juvenile periods and lifespans for serotinous Proteaceae in Moll *et al.* (1980) give a coefficient of 0.11implying that the serotinous species have very short juvenile periods in relation to their lifespans. Data for more shrub species will be needed to confirm that these differences are real.

6.4.5 Dichotomies in life-history traits

A number of different studies have highlighted dichotomies in plant traits which are analogous to those observed in sprouters and seeders (e.g. Keeley 1986, Le Maitre 1992). Caswell (1982) identified ephemeral and persistent life-history strategies; the former is characterised by low investment in defences, short life-span, precocious reproduction and senescence and the latter by the converse traits. He argued that these represent a dichotomy rather than a continuum. Strauss & Ledig (1985) analysed seedling allometry (root:shoot allocations) in pines and characterised them as

either pioneer (low investment in roots and competitiveness) or persistent species (high investment in roots and competitiveness). Loehle (1988) showed that the allometric coefficient of Straus & Ledig (1985) is also related to longevity and argued that at least part of the persistent species' investment was in durable wood and thus in longevity. A graph of Strauss & Ledig's (1985) allometric coefficient against longevity (Loehle 1988 Figure 6.3) clearly shows two groups in the pines: low coefficient and long-lived versus high coefficient and short-lived. Clark's (1991) models offer a sound approach, explicitly based on theories about life-history strategies. His models suggest that underlying reasons for the observed dichotomies in allocation patterns between sprouters and seeders {for example differences in carbon and nutrient allocation (Hansen *et al.* 1991, Pate *et al.* 1991, Bell *et al.* 1996) and in water-use and growth rates (Parker 1984)} are the divergent life-history strategies evolved in response to the selective pressures operating in a given environment: namely opting for a strategy of either (a) persisting and maintaining relatively stable populations with slow growth, or (b) of abandoning persistence for stochastic population fluctuations following disturbances, with a high risk of extinction if fires are too frequent (Bond *et al.* 1995) and the compensation of high population growth rates.

6.5 Conclusions

Clark's (1991) models of the relationships between fire frequency distributions and plant juvenile periods do appear to hold for fynbos species based on the limited data sets investigated in this study. The prediction that juvenile periods, mortality rates and lifespans of seeders with short-lived seed banks and long-lived seeds should differ in several respects have not been borne out completely by the data for the species examined here:

- Species with short-lived seeds do seem to have longer life-spans than species with long-lived seed banks; although mortality rates are significantly higher in old populations of *P. neriifolia* (see also Chapter 2) there is no sudden onset of senescence.
- Species with short-lived seed banks do seem to have lower mean annual mortality rates during the majority of their lifespan than species with long-lived seeds but more data are needed to adequately test this prediction.
- Species with short-lived seed banks do not seem to have longer juvenile periods than those with long-lived seeds suggesting that they are not particularly precocious seed producers.

Clark's (1991) models have proved difficult to apply in this study largely because of difficulties in

Chapter 7: Concluding discussion

The primary aim of this chapter is to summarise the results and shortcomings of the various studies in this thesis and draw some conclusions about the current understanding of the reproductive ecology and population dynamics of the Proteaceae. I also discuss some of the relevant work on life-histories, raise some issues for future research and close with a discussion of some of the implications for management.

7.1 Introduction

I have attempted to unite two fields that have traditionally operated largely independently despite efforts at unification (e.g Harper 1967, 1977), namely population ecology and evolutionary ecology. Population ecology has primarily addressed the proximal issues required to quantify and predict population dynamics within the current *milieu*. It has concentrated on answering the questions: "What? How? When?", but not or only to a limited extent the question: "Why?". Evolutionary ecology has tended to become engrossed in theory, often at the expense of biological reality. This has often led to predictions about life-history traits and strategies which cannot be tested because they were based on inappropriate assumptions or simplifications. Chapters 2-5 of this thesis dealt largely with "here and now" of the reproductive ecology of a number of seed regenerating proteas. In Chapter 6 I tried to show that to ask the question "**Why** do the plants have these demographic trends and associations of traits?" can add perspective and increase our understanding of the underlying driving forces in the system. Loehle & Pechman (1988) make a similar point: that incorporation of the insights offered by evolutionary theory could have provided deeper insights into, and enhanced the predictions of, systems ecology about the structure and functioning of ecosystems. The "r-K" life-history paradigm is an example of a useful construct that provided some important insights into associations of life-history traits, but was generally proved to be inadequate when attempts were made to use it to explain real plant life-histories (e.g. Clark 1991, Ginsburg 1992).

7.2 Key questions

In the introduction I posed some questions which were addressed in different chapters; these are each addressed in turn:

(1) What are the patterns in mortality during the lifetime of serotinous Proteaceae and is there evidence for programmed senescence?

Mortality rates of *Protea lacticolor, P. neriifolia* and *Leucadendron xanthoconus* were relatively high during the first summer after establishment (Chapter 2). In subsequent years the mortality rates were generally lower. Similar patterns have been reported for seed-regenerating, serotinous Proteaceae in shrublands in at other sites in fynbos and in mediterranean Australia (e.g. Bradstock & O'CONNELL 1988; Le Maitre 1992). These findings suggests that Clark's (1991) simplification of mortality to a constant mean rate (exponential) over the majority of the lifespan is appropriate for seeding Proteaceae.

The phenomenon of senescence in seeding Proteaceae has been noted in a number of studies but quantitative data to substantiate these observations, and the implication of a distinct increase in mortality at a particular age, are lacking. An analysis of mortality rates in monitored populations of *Protea lacticolor* and *Leucadendron xanthoconus* (Chapter 2) showed that mortality rates in young (1-10 years) plants are significantly lower than those in old (21-31) plants. A similar significant increase in mortality rates was found when 14-28 and 30-45 year-old *P. neriifolia* populations were compared (Chapter 6). There was little evidence though of an abrupt increase in the mortality rate at a particular age suggesting that the plants lifespan is not fully programmed as implied by the type 1 mortality curve described by Pearl (1927; see also Deevey 1947).

(2) What are the patterns of reproductive maturation and seed bank accumulation in Proteaceae?

A small proportion of *Protea lacticolor, P. neriifolia* and *Leucadendron xanthoconus* plants at Jakkalsrivier matured at 4-5 years of age but 2-3 more years were required for 50% of the populations to produce their first seeds. Presumably because these stands were quite dense (30-60 000 plants/ha, Kruger 1987) seed banks per plant at 10-years of age were low compared with data from other surveys (e.g. Bond 1985). Seed banks of 22 year old *P. lacticolor* and *L. xanthoconus* recorded in a previous study at Jakkalsrivier (Kruger 1987) were substantially greater and highly variable than those of 10-year old plants with 372±572 (S.D.) and 279±342 seeds per plant respectively. Seed banks are unlikely to be sufficient to maintain populations of *P. lacticolor* when fires occur every 10 years or less.

Seed banks of *P. neriifolia* at Swartboskloof accumulated rapidly, giving a mean of 79 seeds per shrub at 8 years of age (Chapter 3), compared with a mean number per shrub of 33 at 10 years of age at Jakkalsrivier, although both populations began flowering at four years of age. A 12 year old *P. neriifolia* stand at Swartboskloof had a mean of 53 seeds per plant and the plants were significantly smaller than a nearby 8 year-old population. This may be because the 12-year old population, like *P.*

neriifolia at Jakkalsrivier, occurred on soils derived from sandstone. Sandstone-derived soils in Swartboskloof are markedly lower in nutrients than the granite derived soils (Fry 1987) where the 8-year old stand occurred. Seed banks in 28-year old stands of *P. repens* and *P. neriifolia* in Swartboskloof (Chapter 3) were more than sufficient for population replacement (observed net recruitment was about 0.2 seedlings per seed, Le Maitre 1992). In *P. neriifolia* stands 8-12 years of age most seeds are in the current crop but in 28-year old plants most seeds were in inflorescences more than two years old.

Co-occurring *Protea nitida,* an epicormically sprouting species which can develop into a small tree, has juvenile periods within an absolute minimum of about 8 years but a more likely period of 15-30 years, especially in areas that are regularly burnt (Le Maitre 1992). Comparable ages at maturity have been reported for morphologically similar sprouting *Banksia* species (Zammit & Westoby 1987b; Lamont & van Leeuwen 1988; Bradstock 1990). *Protea nitida* does not accumulate seed banks (Bond 1985) but flowering is temporally staggered so that some seeds are present on the plant all year round.

(3) How does stand density influence flowering and seed bank accumulation in co-occurring *Protea neriifolia* and *P. repens*?

Increasing stand density resulted in an increasingly skewed size (stem diameter) distribution of *P. neriifolia* and *P. repens* shrubs (Chapter 3). This directly affected inflorescence production because inflorescence production increased exponentially with size. The two species differed in the way in which flower production was influenced by increasing stand density: *P. neriifolia* responded by decreasing the number of inflorescences per shrub and *P. repens* by a decrease in the proportion of shrubs which flowered at all. Maze & Bond (1996) also found that the proportion of sterile shrubs in *P. repens* increased with increasing density. Seed production per shrub followed the same pattern, but there was under-compensation as the numbers of seeds per unit area increased with increasing stand density, as noted also by Esler & Cowling (1990). Maze & Bond (1996) found that the total number of inflorescences in a population decreased with increasing density, but only once parent densities exceeded about 15 000 per hectare for *P. repens* and 6 500 for *P. neriifolia*, higher than the densities recorded at most of the sites in Swartboskloof (Chapter 3). The genetic implications of the highly skewed seed bank distribution are that the gene pools of seedling populations will be dominated by the seeds from a few individuals in the population.

Protea repens produced more seeds per inflorescence than *P. neriifolia* but its seeds decayed faster

so that it had few seeds in older inflorescences whereas most of the seed bank of *P. neriifolia* was in the older inflorescences (Chapter 3). *Protea repens* recruitment therefore is likely to vary more than that of *P. neriifolia* after fires in different seasons. Models for these two species, based on data from a different site, suggest that *P. repens* populations will fluctuate less from generation to generation than those of *P. neriifolia* because inflorescence production by *P. neriifolia* shows greater density dependence (Bond *et al.* 1995). It would be interesting to examine the impacts of combining the effects of both density-dependence and season of burn in a single model.

The use of spatially separated populations of different ages at different sites rather than a true age-series at a site (Chapter 3) always raises the issue of whether the observed patterns are the product of different sites or of site x age interactions rather than age *per se*. This may have had some influence but the general findings are in agreement with those from other sites (e.g. Esler & Cowling 1990; Bond *et al.* 1995; Maze & Bond 1996) suggesting that differences between sites, other than the possible effects of soil differences between one site and the rest (see Chapter 3), have not played a dominant role.

(4) What impacts do pre-dispersal seed predators have on seed bank dynamics, and do patterns in seed set suggest that species differ in their responses to seed predation?

Studies of the impacts of pre-dispersal seed predation in serotinous Proteaceae have shown they vary and that the losses can be high (>40%) (Myburgh *et al.* 1974, Coetzee & Giliomee 1987). Levels of seed predation are inversely correlated with seed set at the population level (Wright 1994) and apparently are reduced by spatial clustering within inflorescences (Mustart *et al.* 1995). Levels of seed predation were high for *P. repens* but were lower in co-occurring *P. neriifolia* in Swartboskloof (Chapter 4). This appears to be related to the relatively high seed set and the more even distribution of seeds among inflorescences in *P. repens* compared with the low seed set and very skewed distribution of seeds between *P. neriifolia* inflorescences. Insects may select *Protea repens* inflorescences because of the greater likelihood of finding seeds for their larvae to feed on. This suggests that selection to minimise seed predation is strong and is expressed at three levels: variation in the seed production of the whole population or stand (possibly environmentally induced), seed number per inflorescence and seed distribution between the inflorescences in a canopy, and seed distribution within the inflorescence. In summary, it seems that seed predation accounts for the majority of the seed losses during storage on the plant, with loss of viability in the inflorescence playing a relatively, and surprisingly, insignificant role (Le Maitre 1990).

The design of this study was not ideal. The decision to investigate the differences in seed predation levels was made when pilot seed collecting work identified some marked differences. Constraints of time and manpower prevented the study from including samples from a greater range of sites and trials of insect exclusion at different stages during flowering. The possibility of an analysis of the feeding tracks of insects and their relationship to the distribution of seeds within the infructescences also had to be ruled out.

(5) How does the temporal distribution of rainfall influence seed germination, and seedling establishment and mortality during the first summer drought?

The temporal distribution of rainfall has a direct impact on germination, with the most rapid germination occurring under the permanently moist conditions prevalent in mid-winter (chapter 8). Although this study used a highly simplified model, the indications are that a moist period of at least four weeks (i.e. soil moisture available and cool conditions for > 45% of the days) is required to ensure successful germination and seedling establishment. These conditions prevailed from May to August but seeds planted after 10 September did not germinate.

Rainfall distribution in time also influences survival during the first summer drought as suggested by Vogts (1982). The timing of germination is the primary factor influencing seedling survival during the first summer after the fire (chapter 8). Percentage survival from 22 October to 23 February was directly related to the number of days between planting and 22 October contrary to the findings of Midgley *et al.* (1989). It seems that increased summer rainfall is likely to enhance seedling survival while a marked decrease is winter and summer rainfall is required to significantly influence seed germination patterns and seedling survival respectively. These are preliminary results and more realistic climate models are required to provide more reliable answers but these are not available yet.

Some similar modelling has been done for Australian Proteaceae. Modelling of the recruitment of *Banksia cuneata* found that recruitment was determined by the temporal patterns in rainfall following a fire and not by seed numbers (Lamont *et al.* 1991a; Burgman & Lamont 1992). This supports Maze and Bond's (1996) finding that protea populations also may not be limited by seed numbers. Dry intervals between rainfall events during the winter and the length of the summer drought were both critical. Bradstock & Bedward (1992) found that time to seedling emergence decreased as the proportion of time in which soils were moist and was also related to temperature, being inhibited by high temperatures. Simulations using extended rainfall records showed that inter-annual variation in recruitment caused by differences in the simulated temporal distributions of rainfall could result in

larger fluctuations in recruitment success than those caused by varying fire season. These findings are very similar to those of Chapter 5, providing additional evidence of the extent of convergence in reproductive ecology between fynbos and kwongan shrublands (Le Maitre & Midgley 1992).

A study which attempts to develop a model of seed germination and seedling establishment and survival ideally should be replicated across years to ensure that the observed patterns are not simply the product of conditions prevailing during that period. The study sites could be visited only at roughly monthly intervals. More robust models could have been developed if observations had been more intensive during seedling emergence (which can be abrupt and highly synchronous Lombaard 1971; Le Maitre & Botha 1991) and during the late-summer when conditions were very hot and dry. The findings of this study appear to contradict those of Midgley *et al.* (1989) and further work is needed to establish if the differences are due to regional differences in climatic conditions, site differences (.e.g soils) or species differences.

(6) Do Clark's (1991) hypotheses about the relationship between fire frequency distributions and seeding and sprouting species ages at first reproduction (juvenile periods) and reproductive lifespans hold for fynbos species?

The two fundamental tenets of life-history theory are that resources are limited and that different life-history traits are directly or indirectly related (Stearns 1976, 1977). Life-history theory has been able to explain some associations between the observed life-history traits, growth and resource allocation in a variety of organisms and in different environments. One of the areas of difficulty has been in finding a suitable basis for modelling the life-histories of species in disturbance driven environments because many of the standard assumptions of life-history theory (e.g. that there is continuous recruitment) are violated. Clark (1991) developed models which accommodate these violations of standard life-history theory and also establish a direct relationship between fire frequency distributions and the age at first reproduction of fire-killed (seeder) and fire-surviving (sprouter) species. Clark's models assume that there is a close correlation between age at first reproduction and the lifespan as suggested by Harper & White (1974) and Loehle (1988). His models further assume that seeding species maximise the probability of being mature at the time of a fire while sprouting species maximise the number of reproductive opportunities in a lifetime. These models were tested using fire frequency data for a number of areas in the fire-prone shrublands (fynbos) of the Western Cape, South Africa, and information on the age at first reproduction, mortality rates and lifespans of a number of Proteaceae species taken from the literature and Chapters in this thesis. Probability distributions with an increasing probability of a fire with increasing post-

fire age (Gamma, Weibull) were found to be more appropriate for fynbos than the Exponential distribution which assumes a constant probability of a fire.

The predicted juvenile periods of *Protea neriifolia,* a seeder with mean annual mortality rates of about 5.6% based on the Gamma distribution were close to those observed in field studies. The predictions for *Orothamnus zeyheri*, a seeder with a relatively high mean mortality rate of 14.8% were much shorter than the observed five years except where there was a low probability of a fire in young vegetation. Predicted juvenile periods based on parameters estimated from exponential distributions fitted to fire-frequency distributions were generally shorter than expected. This was largely because the Exponential distribution overestimates the probability of a fire in young vegetation. The predicted juvenile periods for *Protea nitida*, a sprouter which is relatively fire-sensitive as a seedling or sapling, underestimated the likely primary juvenile period of at least 15 years. The models are sensitive to both the magnitude of the estimated mortality rate (particularly the sprouter model) and the ratio of the juvenile period to the lifespan.

Clark's models appear to hold for fynbos seeders and sprouters. His assumption that sprouters and seeders are following different life-history strategies is supported by a number of other lines of evidence, both physiological and demographic. When compared with co-occurring or related sprouting species, seeders generally: mature earlier and produce more seeds than sprouters (Zammit & Westoby 1987b; Hansen *et al.* 1991; Le Maitre 1992); accumulate larger seed banks than sprouters (Cowling *et al.* 1987; Meney *et al.* 1994); have higher seed germination percentages and seedling recruitment (Keeley & Zedler 1978; Le Maitre 1992); have more rapid seedling growth and higher seedling survival rates (Parker 1984; Zammit and Westoby 1987b); have higher growth and transpiration rates at least as seedlings (Parker 1984); have higher moisture stress resistance (Groom & Lamont 1995; Richards & Lamont 1996); invest less in root systems and reserves stored in root tissues (Pate *et al.* 1990, 1991); have shorter lifespans of 40-50 years whereas co-occurring sprouters appear to have lifespans 2-3 or more times as long (Zammit & Westoby 1987b); mortality rates increase significantly with age from about half the lifespan in seeders but decline with size (and thus age) in spouters like *Protea nitida* (Abbott 1985; Le Maitre 1992; Chapter 6). These differences are all consistent with Williams (1957) hypothesis that senescence is a consequence of selection for early reproduction at the expense of longevity: in fire prone environments selection for early reproduction may have been the driving factor behind the evolution of seed regenerating species.

Unfortunately Clark's models involve some mathematically complex aspects of probability distributions, particularly the use of an optimisation approach based on renewal theory. This

prevented me, for example, from determining what the predicted optimal juvenile period for a sprouter would be when the probability of a fire increases with increasing post-fire age (i.e the frequency distribution is not exponential). Clark (1996) has developed an extension of his models which incorporates seed banks. This looks promising but is based on a generalisation that seed production is a linear function of canopy area and this does not fit the data I have available. Nevertheless, this could be an interesting topic for research and could result in useful model for exploring the implications of changing fire regimes which is based on an understanding of the underlying driving forces rather than just the observed empirical relationships.

7.4 Life-history theory and seeders and sprouters

Some studies have sought analogies in standard life-history theory for the patterns of traits of sprouters and seeders, and the evolution of seeders from sprouters. Because recruitment is effectively restricted to the immediate post-fire environment, seeders can be viewed as analogous to semelparous organisms and sprouters to iteroparous ones (Keeley 1986; Bond 1987; Bond and Van Wilgen 1997). Bond (1987) developed a simple model of the conditions necessary for seeders to evolve from sprouters based on a model developed to explain the evolution of semelparity devised by Charnov & Schaffer (1973). The model requires seeders to recruit sufficient seedlings to compensate for the seedling recruitment of the sprouters *and* the survival of established plants, if they are to have an evolutionary advantage. Expressed in mathematical form (see Bond and van Wilgen 1995):

$$SB\_Sdr * NR\_Sdr > SB\_Spr * NR\_Spr + Spr\_survivors$$

(Spr = sprouter; Sdr = seeder; NR = net recruitment rate; SB = seed bank)

Thus, seeders can gain an advantage by recruiting more seedlings either though larger seed banks (achieved by producing more seeds, or longer-lived seeds, or seeds with a lower mortality during fires) or by having seedlings and juveniles with a higher survivorship, or both (Bond 1987; see also Keeley 1986; Bond and van Wilgen 1995). The critical feature for sprouters is not survival *per se* but survival of seedlings and juveniles through fires until they, in turn, reach maturity. This may require many fire cycles (Bradstock & Myerscough 1988; Bradstock 1990; Le Maitre & Midgley 1992).

Studies following on from Cole's (1954) seminal study show that factors causing greater juvenile than adult mortality favour iteroparity while equal mortality for both stages, or greater adult mortality, favour semelparity (Schaffer & Gadgil 1975; Stearns 1976; Horn 1978). This reasoning

can be applied to seeders and sprouters by viewing them as analogous to semelparous and iteroparous plants, respectively. If greater reproductive success more than compensates for increased adult mortality then selection will favour investing more in offspring rather than in adult longevity. This will favour the evolution of seeders from sprouters. Sprouting will be favoured by conditions where juvenile mortality is higher than adult mortality so that selection favours adult longevity and a long reproductive lifespan. This analogy can be taken further as it predicts that:

- mortality of juvenile and adult seeders in fires should be the same, and numerous studies show that it is in all except cool fires which some adults survive (e.g. *Protea laurifolia*, Le Maitre pers. obs.);
- juvenile plants of sprouters should experience greater fire induced mortality than mature plants. This hypothesis holds for *Protea nitida* where juveniles experience higher mortality rates than adults during fires (Le Maitre & Midgley 1992; Le Maitre 1992; Chapter 6).

Semelparity is also favoured by increasing population growth rates while increasing age of senescence and an increase in the ratio of the primary juvenile period to the period between reproductive episodes favours iteroparity (Young 1981). These predictions are also consistent with the seeder-sprouter analogy outlined above. Seeders produce greater numbers of seedlings than sprouters after fires, while sprouters have long juvenile periods relative to the interval between fires, at least for *Protea nitida* and *P. neriifolia* and other species (Carpenter & Recher 1979; Zammit & Westoby 1987b; Clark 1991; Hansen *et al.* 1991; Pate *et al.* 1991; Le Maitre & Midgley 1992).

As a seeder has only one opportunity to reproduce it has a single lifetime reproductive value which is realised when a fire occurs. Sprouters survive fires and will maximise their fitness by a reproductive value schedule which is maximised over a series of fires. Clark's (1991) models were based on the optimal timing of reproductive maturation and not on maximising the net offspring over a lifetime which is the true measure of fitness. This suggests that by altering Clark's assumptions to read:

- seeders (his type A) maximise their recruitment success by maximising the amount of seeds available when fires are most likely; and
- that sprouters (his type B) maximise their recruitment success by surviving fires and by maximising seedling recruitment over a number of reproductive episodes (fires) during their reproductive lifespan;

the property being maximised is recruitment success and thus evolutionary fitness (see Cole 1954, Taylor *et al.* 1974). Natural selection will favour traits that maximise fitness - sprouters and seeders simply represent two ways to respond to the same environmental pressures - the seeder strategy is high risk and the sprouter strategy is low risk. In many ways this dichotomy is similar to that

between forest and fynbos species, which have very different life-histories and coexist in a dynamic balance in a similar environment (Le Maitre & Midgley 1992; Manders & Richardson 1992). The seeder strategy also has other possible evolutionary advantages which are not described in details here. These include greater opportunities for speciation because of, *inter-alia,* non-overlapping generations and shorter generation times (see Wells 1969) and through population fragmentation due to localised extinctions (Cowling 1987).

7.5 Life-histories and senescence

Theories about senescence can be divided into two groups (Bell 1984): those that ascribe senescence to physiological changes caused by effects of damage and wear at the cell & tissue level, and those ascribing senescence to lack of selective pressure against degeneration in old age or to selection for early reproduction and thus a reduction in the lifespan. As noted earlier, the suites of traits of seeders and sprouters observed in several studies in a variety of fire-prone shrublands are consistent with Williams (1957) hypothesis that senescence (as observed in seeders) is the result of selective pressure for early reproduction at the expense of a greater lifespan. Seeders have to produce seeds by the time a fire occurs if they are to survive that fire; a single failure means extinction and a fitness of zero. The evidence suggests that strong selection for early reproduction was a pre-requisite for the evolution of seeders from sprouters because without a substantial reduction in the juvenile period extinction would be inevitable. The lignotuberous *Leucadendron salignum* and *Mimetes cucullatus* both have relatively short juvenile periods (6-8 years) and also become senescent and exhibit branch die-back in older vegetation (Le Maitre pers. obs.). This suggests that a substantial reduction in investment in stem, branch and height growth may be needed to reduce the juvenile period to close to that of co-occurring seeding species. This trend would be in agreement with Loehle's (1988) argument that the relationship between longevity and juvenile periods in determined, to a large extent, by the costs of producing the durable wood needed to ensure a long lifespan.

7.6 Some issues for future research

A study like this always raises a number of issues and questions that cannot be addressed at the time or which require further study. I have identified a number of these which I believe to be important below.

(1) Seed bank accumulation: As the plant's age increased an increasing proportion of the mature plants failed to flower in all the stands studied for this thesis. The same trends have also been

observed in other serotinous species and it can have a significant impact on seed bank accumulation rates (Kruger & Lamb 1979; Le Maitre *et al.* 1991). The most likely explanation is that this is due to resource limitations although there was no indication of increased inflorescence or seed production in fertilised stands of *Protea repens* (Lamb & Klaussner 1988). Specht's (1963) long-term fertiliser trials suggest that seedlings mature sooner and that their mortality rate is increased but data on lifespans are lacking. Sprouters were apparently less affected. Fertilisation is being increasingly used in cultivation of Proteaceae for cut-flower production. This practice could be used to test whether, for example, reproductive maturity is achieved earlier and if the relationship between the age at reproductive maturation and the lifespan can be altered by reducing the limiting effect of a key resource.

(2) Senescence: Bell (1984) extended William's (1957) hypothesis and suggests that the strength of the selection for senescence should be directly proportional to the genetic difference between parent and offspring. Thus it should be high in species with 'ovigerous' (genetically recombinant) reproduction and low to zero in purely clonal species. This may be difficult to test in long-lived plants but could be an interesting challenge to investigate at the physiological and genetic level to test some of the non-evolutionary theories of senescence from an evolutionary perspective.

(3) Sprouters and seeder life-histories: Clark (1991) **assumed** that seeders maximise the **probability** that they will be reproductively mature when a fire comes; that sprouters maximise the **number** of reproductive episodes over the lifespan. Extension of these models to include seed banks could provide a test of my proposal that an investigation of the relative fitness (i.e. net seedling recruitment see Taylor *et al.* 1974) of these two life-histories could show that they are alternative ways of maximising reproductive success. This would recast these assumptions in a form in which the property being maximised is evolutionary fitness and would facilitate direct tests, which could show that the assumptions are not necessary.

(4) This study examined the implications of fire frequency for plant life-history traits. If Clark's (1991) approach is developed further to include seed banks (as suggested above) this would allow for more detailed modelling of the effects of varying the fire frequency and the season of burn.

(5) In chapter 6 I also examined the possibility that species with long and short-lived seed banks would differ in their juvenile periods, mortality rates and lifespans. The analysis found that they differed as expected in the last two traits but not in the first one. This pattern could be explained if the species with long-lived seeds benefited from delayed maturity, or the species with short-lived seeds benefited from precocious maturation. Delayed maturation is generally held to be advantageous if it leads to greater reproductive allocation (e.g. Cohen 1971). This possibility could be tested relatively easily.

(6) This study did not examine competition between seeders and sprouters and life-history traits

which would allow seeder seedlings to outcompete sprouter seedlings although studies of allocation patterns (e.g. Pate *et al.* 1990) suggest that seeders would have a competitive advantage in above ground growth. Bond and Midgley (1995) have revived Mutch's (1970) hypothesis that plants in fire-prone environments are adapted to burn and argue that a key ingredient is seeder seedling competitiveness. Serotinous species typically occur in dense stands, a trait that would favour intense fires (Lamont *et al.* 1991b). Is serotiny also associated with other traits that would, for example, minimise competition in these stands or maintain high seed or seedling densities?
(7) Why are tall, epicormically sprouting species relatively rare in fynbos compared with kwongan when the suites of life-story traits are so strikingly similar in many other ways (Le Maitre & Midgley 1992)?

7.7 Some implications for management

A major goal of conservation management in the fynbos is to maintain the ecological functioning and genetic diversity of natural ecosystems in conservation areas. This goal can only be achieved if there are sound guidelines to assist management personnel in decisions about management policies and actions. At present, management decisions are based on a set of general policy guidelines and a limited amount of field data. Fynbos will burn under extreme conditions at an age of 4-6 years but in most cases ecological considerations limit burning until the vegetation is 12-15 years old (Van Wilgen *et al.* 1992). Therefore there is an interval of 8-11 years during which the vegetation can burn. In many cases managers also need to take weed control operations into account. The major weeds in fynbos are all well adapted to increase after fires so that control measures must be implemented before burning (Van Wilgen *et al.* 1992). The final management consideration is to plan burning operations to obtain a mosaic of vegetation patches of different ages to facilitate fire control operations.

Management is greatly simplified if definite and narrow prescriptions can be given. Research findings indicate clearly though that in systems that are so strongly dominated by seeders that a large number of factors are really out of the manager's control. Managers can manipulate fire frequency, season and intensity but the rainfall amount and distribution during the winter and first summer that follow fire are not controllable. Nevertheless the risk of recruitment failure could be much greater after fires in a season when recruitment is expected to be poor (winter or spring). Continuous burning in the optimal season could result in very dense populations which could suppress understorey species and be detrimental in the long term (Cowling & Gxaba 1990), but it is more likely that natural variation in stand densities from fire to fire would allow other species to persist.

The implications of these ideas for management policies are that fluctuations are a necessary and vital part of fynbos communities and that management operations should not be directed towards achieving some fixed 'golden rule'. In practice, the variety of uncontrollable factors and unplanned fires introduce an unpredictable element which prevents the achievement of any such 'golden rule'. Studies of lottery models also suggest that there are limits to the resilience of the system beyond which species can go extinct. Some of these are well documented in fynbos. Winter or spring fires and high or low fire frequencies can lead to the extinction of serotinous Proteaceae and other species (Bond 1980; Van Wilgen 1981). A sound understanding of the limits to the resilience of species is essential when managing fragmented habitats, such as lowland fynbos (Cowling 1987), because they cannot recolonise patches after becoming extinct. This is particularly important because seedling regeneration is the critical stage in the life of seeding plants (Parker 1984; Bond 1989). Decisions about when and how to burn areas should be based on developing an understanding of the vegetation and by intelligent application of simple 'rules of thumb' such as that for the minimum age at which a population of a serotinous species can safely be burnt: at least half the population must have flowered for three or more seasons (Kruger & Lamb 1979; Van Wilgen *et al.* 1992).

7.8 Postscript

I believe that the studies in this thesis demonstrate that studies of the demography of species can be much more informative when they are linked to the insights provided by life-history theory. Clark's life-history models appear to provide a workable basis which allows formal analyses to progress beyond the limitations the 'r-K' life-history modelling. Studies of the life-histories of long-lived plants of the kind included in this thesis require data from long-term modelling studies. One of the tragedies of the current loss of expertise from conservation agencies is the collapse of most of the organised plant population monitoring programmes which were initiated in fynbos vegetation in the 1970's. This is not a recent development, all of the studies which provided the data for some of the chapters of this thesis were abandoned in the late 1980s. This means that the very information that is vital for understanding resilience is no longer being gathered.

The key ingredient in re-establishing long-term studies will be constructive interactions between the managers, particularly senior managers, and researchers. Workshops provide an ideal opportunity for interaction between all the different parties with an interest in fynbos, for example those organised by the Fynbos Forum. One of the key issues that needs to be debated is the importance of well designed, long-term studies. At present these are generally dismissed as too costly or too difficult to maintain, but this needs to be weighed up against the fact that they are the only way to

obtain some of the data needed to ensure that management activities are achieving their goals of long-term maintenance of biodiversity.

Lastly, I would like to emphasise that managers can become more closely acquainted with their flora and fauna than anyone else. By following their natural curiosity and adding to it careful observation, keeping accurate records and asking intelligent questions - like Rudolph Marloth who was probably South Africa's greatest naturalist - they can play a significant role in enhancing our understanding of the unique and often enigmatic ecology of fynbos.

References

Abbott I 1985. Reproductive ecology of *Banksia grandis* (Proteaceae). *New Phytologist* 99: 129-148.

Alcamo, J, van den Born G, Bouwman AF, De Haan BJ, Kelien Goldewijk K, Klepper O, Krabec J, Leemans R, Olivier JGJ, Toet AM, de Vries HJM & van der Woerd HJ 1994. Modeling the global society-biosphere-climate system: part 2: computed scenarios. In: *Image 2.0: Integrated modeling of global climate change* (ed. Alcamo J), pp 37-78. Kluwer Academic Publishers, Dordrecht.

Andersen AN 1989. Impact of insect predation on ovule survivorship in *Eucalyptus baxteri*. *Journal of Ecology* 77: 62-69.

Angevine MW 1983. Variations in the demography of natural populations of the wild strawberries *Fragraria vesca* and *F. virginica*. *Journal of Ecology* 71: 959-974.

Aschmann H 1973. Distribution and peculiarity of mediterranean ecosystems. In: *Mediterranean-type ecosystems, origin and structure* (eds di Castri F & Mooney HA), pp 11-19. Chapman & Hall, London.

Augspurger CK 1981. Reproductive synchrony of a tropical shrub: experimental studies on effects of pollinators and seed predators on *Hybanthus prunifolius* (Violaceae). *Ecology* 62:775-788.

Auld, TD 1987. Population dynamics of the shrub *Acacia suaveolens* (Sm.) Willd.: Survivorship throughout the life-cycle, a synthesis. *Australian Journal of Ecology* 12: 139-151.

Ayre DJ & Whelan RJ 1989. Factors controlling fruit set in hermaphroditic plants: studies with the Australian Proteaceae. *Trends in Ecology & Evolution* 4: 267-272.

Bart J & Robson DS 1982. Estimating survivorship when the subjects are visited periodically. *Ecology* 63: 1078-1090.

Bawa KS & Webb CJ 1984. Flower, fruit and seed abortion in tropocal forest trees: implications for the evolution of paternal and maternal reproductive patterns. *American Journal of Botany* 71: 736-751.

Bawa KS, Hedge SG, Ganeshaiah KN & Shaanker RU 1989. Embryo and seed abortion in plants. *Nature* 342: 625.

Begon M, Harper JL & Townsend CR 1986. Ecology: individuals, populations and communities. Blackwell Scientific Publications, Oxford.

Bell DT, Plummer JA & Taylor SK 1993. Seed germination ecology in southwestern Western Australia. *The Botanical Review* 59: 24-73.

Bell G 1984. Evolutionary and nonevolutionary theories of senescence. *American Naturalist* 124: 600-603.

Bell TL, Pate JS & Dixon KW 1996. Relationships between fire response, morphology, root anatomy and starch distribution in south-western Australian Epacridaceae. *Annals of Botany* 77: 357-364.

Bendel RB, Higgins SS, Teberg JE & Pyke DA 1989. Comparison of skewness coefficient, coefficient of variation, and Gini coefficient as inequality measures within populations. *Oecologia* 78: 394-400.

Betts RA, Cox PM, Lee SE & Woodward FI 1997. Contrasting physiological and structural vegetation feedbacks in climate change simulations. *Nature* 387: 796-799.

Bishop GF, Davy AJ & Jefferies RL 1978. Demography of *Hieracium pilosella* in a Breck grassland. *J. Ecol.* 66: 615-629.

Bond WJ 1980. Fire and senescent fynbos in the Swartberg, Southern Cape. *South African Forestry Journal* 114: 68-74.

Bond WJ 1984. Fire survival of Cape Proteaceae - influence of fire season and seed predators. *Vegetatio* 56: 65-74.

Bond WJ 1985. Canopy-stored seed reserves (serotiny) in Cape Proteaceae. *South African Journal of Botany* 51: 181-186.

Bond WJ 1987. Regeneration and its importance in the distribution of woody plants. Ph.D. Thesis, University of California, Los Angeles.

Bond WJ 1989. The tortoise and the hare: the ecology of angiosperm dominance and gymnosperm persistence. *Biological Journal of the Linnaean Society* 36: 227-249.

Bond WJ & Breytenbach GJ 1985. Ants, rodents and seed predation in Proteaceae. *South African Journal of Zoology* 20: 150-154.

Bond WJ & Midgley JJ 1995. Kill thy neighbour: an individualistic argument for the evolution of flammability. *Oikos* 73: 79-85.

Bond WJ & Richardson DM 1990. What can we learn from extinctions and invasions about the effects of climate change? *South African Journal of Science* 86: 429-433.

Bond WJ & Van Wilgen BW 1996. *Fire and plants*. Chapman & Hall, London.

Bond WJ, Cowling RM & Richards MB 1992. Competition and coexistence. In: *The ecology of fynbos: fire, nutrients and diversity* (ed. Cowling R M), pp 206-225. Oxford University Press, Cape Town.

Bond WJ, Maze K & Desmet P 1995. Fire, life-histories and the seeds of chaos. *Ecoscience* 2: 252-260.

Bond WJ, Vlok J & Viviers M 1984. Variation in seedling recruitment of Cape Proteaceae after fire. *Journal of Ecology* 72: 209-221.

Botha SA & Le Maitre DC 1992. Effects of seed and seedling predation by small mammals on seedling recruitment of *Protea neriifolia* in Swartboskloof, Cape Province. *South African Journal of Zoology* 27: 60-69.

Boucher C 1980. Orothamnus zeyheri - interim report January 1980. Unpublished report, Jonkershoek Forestry Research Centre.

Boucher C 1981. Autecological and population studies of Orothamnus zeyheri in the Cape of South Africa. In: *The biological aspects of rare plant conservation* (ed. Synge H), pp 343-353. J Wiley and Sons Ltd., London.

Bradshaw AD 1972. Some of the evolutionary consequences of being a plant. *Evolutionary Biology* 5: 25-47.

Bradstock RA 1990. Demography of woody plants in relation to fire: *Banksia serrata* Lf. and *Isopogon anemonifolius* (Salisb.) Knight. *Aust. J. Ecol.* 15: 117-132.

Bradstock RA & Bedward M 1992. Simulation of the effect of season of fire on post-fire seedling emergence of two *Banksia* species based on long-term rainfall records. *Australian Journal of Botany* 40: 75-88.

Bradstock RA & Myerscough PJ 1981. Fire effects on seed release and the emergence and establishment of seedlings in *Banksia ericifolia* L.f. *Australian Journal of Botany* 29: 521-531.

Bradstock RA & Myerscough PJ 1988. The effects of frequent fires on recruitment and survival in woody resprouters: *Banksia serrata* and *Isopogon anemonifolius*. *Australian Journal of Botany* 36: 415-31.

Bradstock RA & O'Connell MA 1988. Demography of woody plants in relation to fire: *Banksia ericifolia* L.f. and *Petrophile pulchella* (Schrad.) R.Br. *Australian Journal of Ecology* 13: 505-518.

Bradstock RA, Gill AM, Hastings SM & Moore PHR 1994. Survival of serotinous seedbanks during bushfires: comparative studies of *Hakea* species from southeastern Australia. *Australian Journal of Ecology* 19: 276-282.

Breytenbach GJ 1982. Small mammal responses to environmental gradients in the Groot Swartberg of the southern Cape. M.Sc. thesis, University of Pretoria.

Breytenbach GJ 1984. Single agedness in fynbos: A predation hypothesis. In: *Proceedings of the 4th international conference on mediterranean ecosystems* (ed.) Dell B, pp 14-15. University of Western Australia, Nedlands, Australia.

Brits GJ 1986. Influence of fluctuating temperatures and H_2O_2 treatment on germination of *Leucospermum cordifolium* and *Serruria florida* (Proteaceae) seeds. *South African Journal of Botany* 52: 286-290.

Brits GJ 1987. Germination depth vs. temperature requirements in naturally dispersed seeds of *Leucospermum cordifolium* and *L. cuneiforme* (Proteaceae). *South African Journal of Botany* 53: 119-124.

Brits GJ & Van Niekerk MN 1986. Effects of air temperature, oxygenating treatments and low temperature on seasonal germination response of *Leucospermum cordifolium* (Proteaceae). *South African Journal of Botany* 52: 207-211.

Brown PJ, Manders PT, Bands DP, Kruger FJ & Andrag RH (1991). Prescribed burning as a conservation management practice: a case history from the Cederberg, South Africa. *Biological Conservation* 56: 133-150.

Burgman MA & Lamont BB 1992. A stochastic model for the variability of *Banksia cuneata* populations: environmental, demographic and genetic effects. *Journal of Applied Ecology* 29: 719-727.

Carpenter FL & Recher HF 1979. Pollination, reproduction and fire. *American Naturalist* 113: 871-879.

Caswell H 1982. Stable population structure and reproductive value for populations with complex life-cycles. *Ecology* 63: 1223-1231.

Catana AJ 1963. The wandering quarter method of estimating population density. *Ecology* 44: 349-360.

Caughley G 1978. *Analysis of vertebrate populations*. John Wiley & Sons, London.

Cavers PB 1983. Seed demography. *Canadian Journal of Botany* 61: 3578-3590.

Charnov EL & Schaffer WM 1973. Life-history consequences of natural selection: Cole's result revisited. *American Naturalist* 107: 791-3.

Cheney NP 1981. Fire behaviour. In: *Fire and the Australian biota* (eds Gill AM, Groves RH & Noble IR). Australian Academy of Science, Canberra.

Chesson PL 1986. Environmental variation and the coexistence of species. *Community Ecology* (Eds J Diamond & TJ Case) pp 240-256. Harper & Row, New York.

Chesson PL & Warner RR 1981. Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist* 117: 923-43.

Christensen NL 1985. Shrubland fire regimes and their evolutionary consequences. In: *The ecology of natural disturbance and patch dynamics* (eds Pickett S T A & White P S). Academic Press, New York. pp 86-100.

Clark JS 1989. Ecological disturbance as a renewal process: theory and application to fire history. *Oikos* 56: 17-30.

Clark JS 1991. Disturbance and tree life history on the shifting mosiac landscape. *Ecology* 72: 1102-1118.

Clark JS 1996. Testing disturbance theory with long-term data: alternative life-history solutions to the distribution of events. *American Naturalist* 148: 976-996.

Clements FE 1916. Plant succession: an analysis of the development of vegetation. Publication No. 242, Carnegie Institute of Washington.

Clifford AC 1965. Maximum likelihood estimation in the Weibull distribution based on complete and on censored samples. *Technometrics* 7: 579-588.

Cody ML 1966. A general theory of clutch size. *Evolution* 20: 174-84.

Cody ML 1986. Structural niches in plant communities. *Community Ecology* (Eds J Diamond & TJ Case) pp 381-405. Harper & Row, New York.

Cody ML & Mooney HA 1978. Convergence versus non-convergence in mediterranean-climate ecosystems. *Annual Review of Ecology & Systematics* 9: 265-321.

Coetzee JH 1984. Insekte in assosiasie met *P. repens* (L.)L. M.Sc. Thesis, University of Stellenbosch.

Coetzee JH & Giliomee JH 1987. Seed predation and survival in the infructescences of *Protea repens* (Proteaceae). *South African Journal of Botany* 53: 61-64.

Cohen AC 1965. Maximum likelihood estimation in the Weibull distribution based on complete and on censored samples. *Technometrics* 7: 579-588.

Cohen D 1968. A general model of optimal reproduction. *Journal of Ecology* 56: 219-228.

Cole LC 1954. The population consequences of life-history phenomena. *Quarterly Review of Biology* 29: 103-137.

Collins BG & Rebelo AG 1987. Pollination biology of the Proteaceae in Australia and southern Africa. *Australian Journal of Ecology* 12: 387-421.

Copland BJ & Whelan RJ 1989. Seasonal variation in flowering intensity and pollination limitation of fruit set in four co-occurring *Banksia* species. *Journal of Ecology* 77: 509-523.

Cowling RM 1987. Fire and its role in coexistence and speciation in Gondwana shrublands. *South African Journal of Science* 83: 106-111.

Cowling RM & Lamont BB 1987. Post-fire recruitment of four co-occurring *Banksia* species. *Journal of Applied Ecology* 24: 645-658

Cowling RM & Gxaba T 1990. Variation in post-fire recruitment of a fynbos overstorey shrub: effects on understorey community structure and implications for community-wide species richness. *South African Journal of Ecology* 1: 1-7.

Cowling RM, Lamont BB & Pierce SM 1987. Seed bank dynamics of four co-occurring *Banksia* species. *Journal of Ecology* 75: 289-302.

Cowling RM, Lamont BB & Enright NJ 1990. Fire and management of south-western Australian banksias. *Proceedings of the Ecological Society of Australia* 16: 177-183.

Cowling RM, Witkowski ETF, Milewski AV & Newbey KR 1994. Taxonomic, edaphic and biological aspects of narrow plant endemism on matched sites in mediterranean South Africa and Australia. *Journal of Biogeography* 21: 651-664.

Cox DR 1962. *Renewal theory*. Methuen & Co Ltd, London.

Daniel WW 1978. *Applied nonparametric statistics*. Houghton Mifflin Company, Boston.

Deall GB & Brown NAC 1981. Seed germination in *Protea magnifica* Link. *South African Journal of Science* 77: 175-176.

Deacon HJ 1992. Human settlement. In: *The ecology of fynbos: nutrients, fire and diversity* (ed. RM Cowling), pp 260-270. Oxford University Press, Cape Town.

Deevey ES 1947. Life tables for natural populations of animals. *Quarterly Review of Biology* 22: 283-314.

Diamond J & Case TJ (eds) 1986. *Community Ecology*. Harper and Row, New York.

Di Castri F & Mooney HA 1973. *Mediterranean ecosystems: origin and structure*. Springer-Verlag, Berlin.

Easterling, DR, Horton B, Jones PD, Peterson TC, Karl TR, Parker DE, Salinger MJ, Razuvayev V, Plummer N, Jamason P & Folland, CK 1997. Maximum and minimum temperature trends for the globe. *Science* 277: 364-367.

Enright NJ & Lamont BB 1989. Seed banks, fire season, safe sites and seedling recruitment in five co-occurring *Banksia* species. *Journal of Ecology* 77: 1111-22.

Enright NJ & Lamont BB 1992. Recruitment variability in the resprouting shrub *Banksia attentuata* and non-sprouting congeners in the northern scrub-heaths of south-western Australia. *Acta Oecologia* 13: 727-741.

Enright NJ, Lamont BB & Marsula R 1996. Canopy seed bank dynamics and optimum fire regime for the highly serotinous shrub, *Banksia hookeriana*. *Journal of Ecology* 84: 9-17.

Esler KJ & Cowling RM 1990. Effects of density on the reproductive output of *Protea lepidocarpodendron* (L.)L. *South African Journal of Botany* 56: 29-33.

Esler KJ, Cowling RM, Witkowski ETF & Mustart PJ 1990. Reproductive traits and accumulation of nitrogen and phosphorus during the development of fruits of *Protea compacta* (calcifuge) and *P. obtusifolia* Buek ex Meisn (calcicole). *New Phytologist* 112: 109-115.

Fitter AH 1986. Aquisition and utilization of resources. In: *Plant ecology* (ed. M J Crawley), pp 375-406. Blackwell Scientific Publications, Oxford, England.

Forcella F 1980. Cone predation by pinyon cone beetle (*Conophthorous edulis*; Scolytidae): dependence on frequency and magnitude of cone production. *American Naturalist* 116: 594-598.

Fry M St L 1987. A detailed characterization of soils under different fynbos-climate-geology combinations in the south-western Cape. Unpublished M.Sc. Thesis, University of Stellenbosch.

Fuggle RF 1981. Macro-climatic patterns within the fynbos biome. National Programme for the Environmental Science, Fynbos Biome Project, Final Report. CSIR Pretoria.

Gill AM 1975. Fire and the Australia flora: a review. *Australian Forestry* 38: 4-25.

Gill AM & McMahon A 1986. A post-fire chronosequence of cone, follicle and seed production in Banksia ornata. *Australian Journal of Botany* 34: 425-433.

Gill DE 1978. On selection at high population density. *Ecology* 59: 1289-91.

Ginsburg LR 1992. Evolutionary consequences of basic growth equations. *Trends in Ecology & Evolution* 7: 133.

Grime JP 1979. Plant strategies and vegetation processes. John Wiley, Chichester.

Groom PK & Lamont BB 1995. Leaf morphology and life form influence water relations of *Hakea* species on different soil substrates within southwestern Australia. *Acta Oecologia* 16: 609-620.

Groom PK & Lamont BB 1996. Reproductive ecology of non-sprouting and resprouting species of *Hakea* in southwestern Australia. In: *Gondwanan heritage: past, present and future of the Western Australian biota* (ed. Hopper SD), pp 239-248. Surrey, Beaty & Sons, Chipping Norton, Australia.

Grubb PJ 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Review* 52: 107-145.

Grubb PJ 1988. The uncoupling of disturbance and recruitment, two kinds of seed bank, and persistence of plant populations at the regional and local scales. *Annali Zoologici Fennici* 25: 23-26.

Haig D & Westoby M 1988. On limits to seed production. *American Naturalist* 131: 757-759.

Hansen A, Pate JS & Hansen AP 1991. Growth and reproductive performance of a seeder and a resprouter species of *Bossiaea* as a function of plant age after fire. *Annals of Botany* 67: 497-509.

Harper JL 1967. A Darwinian approach to plant ecology. *Journal of Applied Ecology* 4: 267-290.

Harper JL 1977. *The population biology of plants*. Academic Press, New York.

Harper JL & White J 1974. The demography of plants. *Annual Review of Ecology & Systematics* 5: 419-63.

Haynes RA 1976. Aspects of the life-history and ecology of *Protea arborea* Houtt. Project Report, Field ecology course, University of Zimbabwe, Harare.

Head MJ & Lacey CJ 1988. Radiocarbon age determinations from lignotubers. *Australian Journal of Botany* 36: 93-100.

Heydecker W & Coolbear P 1977. Seed treatments for improved performance - survey and attempted prognosis. *Seed Science and Technology* 5: 353-425.

Hilbert DW 1987. A model of life-history strategies of chaparral shrubs in relation to fire frequency. In: *Plant response to stress - functional analysis in mediterranean ecosystems* (eds Tenhunen J D, Catarino F M, Lange OL & Oechel WC). Springer Verlag, Berlin.

Horn HS 1978. Optimal tactics of reproduction and life-history. In: Krebs J R & Davies N B (eds.) *Behavioural ecology- an evolutionary approach*, pp 41-49. Blackwell Scientific Publications, Oxford, England.

Horn W 1962. Breeding research in South African plants: II. Fertility of Proteaceae. *Journal of South African Botany* 28: 259-268.

Horne, IP 1981. The frequency of veld fires in the Groot Swartberg Mountain Catchment Area. *South African Forestry Journal* 118: 56-60.

Hudson DA 1997. Southern African climate change simulated by the GENESIS GCM. *South African Journal of Science* 93: 389-403.

Hulme M, Conway AJ & Mulenga H 1996. A 1961-90 climatology for Africa south of the equator and a comparison of potential evapotranspiration rates. *South African Journal of Science* 92: 334-343.

Hutchings MJ, Booth KD & Waite S 1991. Comparison of survivorship by the logrank test: criticisms and alternatives. *Ecology* 72: 2290-2293.

Janzen DH 1971. Seed predation by animals. Annual Review of Ecology and Systematics **2**:465-492.

Johnson EA 1979. Fire recurrence in the subarctic and its implications for vegetative composition. *Canadian Journal of Botany* 57: 1374-1379.

Johnson EA & Gutsell SL 1994. Fire frequency models, methods and interpretations. *Advances in Ecological Research* 25: 239-287.

Johnson EA & van Wagner CE 1985, The theory and use of two fire history models. *Canadian Journal of Forest Research* 15: 214-220.

Johnson NL & Kotz S 1970. *Distributions in Statistics. Continuous Univariate Distributions - 1.* Houghton Mifflin Company, Boston.

Jongens-Roberts SM & Mitchell DT 1986. The distribution of dry mass and phosphorus in an evergreen fynbos shrub species, *Leucospermum parile* (Salisb. ex J. Knight) Sweet (Proteaceae), at different stages of development. *New Phytologist* 103: 669-683.

Jordaan PG 1944. Die morfologie van die saadknop van Suid-Afrikaanse Proteaceae. D.Sc. Thesis, University of Stellenbosch, Stellenbosch.

Jordaan PG 1949. Aantekeninge oor die voortplanting en brand periodes van *Protea mellifera* Thunb. *Journal of South African Botany* 15: 121-5.

Jordaan PG 1965. Die invloed van 'n winterbrand op die voortplanting en brandperiodes van *Protea mellifera* Thunb. *Tydskrif vir Natuurwetenskappe* 5: 27-31.

Joubert DA & Tyson PD 1997. Equilibrium and fully coupled GCM simulations of southern African climates. *South African Journal of Science* 93: 471-484.

Keeley JE 1977. Seed production, seeds populations in soil, and seedling production after fire for two congeneric pairs of sprouting and seeding shrubs. *Ecology* 58: 820-829.

Keeley JE 1986. Resilience of mediterranean shrub communities to fires. In: *Resilience in mediterranean-type ecosystems* (eds Dell B, Hopkins A J M & Lamont B B). Dr W Junk Publishers, Dordrecht. pp 95-112.

Keeley JE & Keeley SC 1977. Energy allocation patterns of a sprouting and a non-sprouting species of *Arctostaphylos* in the California chaparral. *American Midland Naturalist* 98: 1-10.

Keeley JE & Zedler PH 1978. Reproduction of chaparral shrubs after fire: a comparison of sprouting and seeding strategies. *American Midland Naturalist* 99: 142-161.

Keith DA & Bradstock RA 1994. Fire and competition in Australian heath: a conceptual model and field investigations. *Journal of Vegetation Science* 5: 347-354.

Kozlowski J 1993. Optimal allocation of resources to growth and reproduction: implications for age and size at maturity. *Trends in Ecology & Evolution* 7: 15-19.

Kruger FJ 1974. The physiography and plant communities of Jakkalsrivier catchment. M.Sc. Thesis, University of Stellenbosch, Stellenbosch.

Kruger FJ 1979. Fire. In: Fynbos ecology: a preliminary synthesis (eds. J Day, WR Siegfried, GN Louw & ML Jarman), pp 43-57. SANSP Report No. 40, Foundation for Resarch Development, Pretoria.

Kruger FJ 1983. Plant community diversity and dynamics in relation to fire. In: *Mediterranean-type ecosystems: The role of nutrients* (eds. Kruger F J, Mitchell D T & Jarvis J U M), pp. 466-72. Springer Verlag, Berlin.

Kruger FJ 1987. Succession after fire in selected fynbos communities of the south-western Cape. Ph.D. thesis, University of the Witwatersrand.

Kruger FJ & Bigalke RC 1984. Fire in fynbos. In: *Ecological effects of fire in South African ecosystems* (eds PDeV Booysen & NM Tainton) pp 67-114. Springer-Verlag, Berlin.

Kruger FJ & Lamb AJ 1979. Conservation of the Kogelberg State Forest. Preliminary assessment of the effects of management from 1967 to 1978. Interim report on project 1/3/11/07. Jonkershoek Forestry Research Centre Report No 79-02.

Kruger FJ, Mitchell DT & Jarvis JUM (eds) 1983. *Mediterranean-type ecosystems: The role of nutrients*. Springer Verlag, Berlin.

Kummerow J, Montenegro G & Krause D 1981. Biomass, phenology and growth. In: *Resource use by chaparral and matorral: a comparison of vegetation function in two mediterranean type ecosystems*, (ed. Miller PC), pp 69-96. Springer-Verlag, Berlin.

Kuo J, Hocking PJ & Pate JS 1982. Nutrient reserves in seeds of selected proteaceous species from south-western Australia. *Australian Journal of Botany* 30: 231-249.

Lamb AJ & Klaussner E 1988. Response of the fynbos shrubs *Protea repens* and *Erica plukenetii* to low levels of nitrogen and phosphorous applications. *South African Journal of Botany* 54: 558-564.

Lamont BB & Barker MJ 1988. Seed bank dynamics of a serotinous, non-sprouting Banksia. *Australian Journal of Botany* 36: 193-203.

Lamont BB & Barrett GJ 1988. Constraints on seed production and storage in a root-suckering *Banksia*. *Journal of Ecology* 76: 1069-1082.

Lamont BB & Markey A 1995. Biogeography of fire-killed and resprouting *Banksia* species in south-western Australia. *Australian Journal of Botany* 43: 283-303.

Lamont, BB & van Leeuwen, SJ 1988. Seed production and mortality in a rare *Bansksia* species. *Journal of Applied Ecology* 25: 551-559.

Lamont BB & Witkowski ETF 1995. A test for lottery recruitment among four *Banksia* species based on their demography and biological attributes. *Oecologia* 101: 299-308.

Lamont BB, Collins BG & Cowling RM 1985. Reproductive ecology of the Proteaceae in Australia and South Africa. *Proceedings of the Ecological Society of Australia* 14: 213-224

Lamont BB, Connel S & Bergl S 1991a. Seed bank and population dynamics of *Banksia cuneata*: the role of time, fire, and moisture. *Botanical Gazette* 152: 114-122.

Lamont BB, Le Maitre DC, Cowling RM & Enright NJ 1991b. Canopy seed storage in woody plants. *Botanical Review* 57: 277-317.

Lamont BB, Witkowski ETF & Enright NJ 1993. Post-fire litter microsites: safe for seeds, unsafe for seedlings. *Ecology* 74: 501-512.

Laurie H & Cowling RM 1994. Lottery coexistence models extended to plants with disjoint generations. *Journal of Vegetation Science* 5: 161-168.

Laurie H, Mustart P & Cowling RM 1997. A shared niche? The case of the species pair *Protea obtusifolia - Leucadendron meridianum*. *Oikos* 79: 127-136.

Law R 1979. The cost of reproduction in an annual meadow grass. *American Naturalist* 113: 3-16.

Law R 1981. The dynamics of a colonising population of *Poa annua*. *Ecology* 62: 1267-1277.

Lawless JF 1982. *Statistical models and methods for lifetime data*. John Wiley & Sons, New York.

Le Maitre DC 1987a. The effects of parent plant density and fire season on the regeneration of *Leucadendron laureolum* (Proteaceae) in the Kogelberg. *South African Journal of Botany* 55: 581-4.

Le Maitre DC 1987b. Dynamics of canopy-stored seed in relation to fire. In: Disturbance and the dynamics of fynbos communities (eds RM Cowling, DC Le Maitre, B Mackenzie, RP Prys-Jones & BW Van Wilgen), pp 24-45. S.A.N.S.P. Report No 135, June 1987, Foundation for Research Development, Pretoria.

Le Maitre DC 1990. The influence of seed ageing on the plant on seed germination *Protea neriifolia* R.Br. (Proteaceae). *South African Journal of Botany* 56: 49-53.

Le Maitre DC 1992. The relative advantages of seeding and sprouting in fire-prone environments: a comparison of life histories of *Protea neriifolia* and *Protea nitida*. In: *Fire in South African mountain fynbos: ecosystem, community and species response to fire at Swartboskloof* (eds van Wilgen BW, Richardson DM, Kruger FJ & van Hensbergen HJ), pp 121-144. Springer-Verlag, Berlin.

Le Maitre DC & Botha SA 1991. Short communication: The effects of exposure to different environments on the viability of *Protea neriifolia* seeds. *South African Journal of Botany* 57: 226-8.

Le Maitre DC & Botha SA 1994. Selective predation on *Protea neriifolia* seeds by small mammals. *South African Journal of Zoology* 29: 191-194.

Le Maitre DC & Midgley JJ 1991. Allometric relationships between leaf and inflorescence mass in the genus *Protea* (Proteaceae): an analysis of the exceptions to the rule. *Functional Ecology* 5: 476-484.

Le Maitre DC & Midgley JJ 1992. Plant reproductive ecology. In: *The ecology of fynbos: fire, nutrients and diversity* (ed. RM Cowling), pp. 135-174. Oxford University Press, Cape Town.

Le Maitre DC, Lamb AJ & Jones CA 1991. Conservation of the Kogelberg State Forest: an assessment of management from 1967 to 1988. Unpublished report Jonkershoek Forestry Centre, Stellenbosch.

Leverich WJ & Levin DA 1979. Age-specific survivorship and reproduction in *Phlox drummondii*. *American Naturalist* 113: 881-903.

Levins R 1966. The strategy of model building in population biology. *American Scientist* 54: 421-431.

Linacre ET 1977. A simple formula for estimating evaporation rates in various climates using temperature data alone. *Agricultural Meteorology* 18: 409-424.

Lloyd DG 1980. Sexual strategies in plants. 1. An hypothesis of serial adjustment of material investment during one reproductive season. *New Phytologist* 6: 69-79.

Loehle C 1988. Tree life-history strategies: the role of defences. *Canadian Journal of Forest Research* 18: 209-222.

Loehle C & Pechmann JHK 1988. Evolution, the missing ingredient in systems ecology. *American Naturalist* 132:884-899.

Lombaard HB 1971. 'n Ekologiese studie van aspekte van die generatiewe voortplanting van *Protea mellifera* en *Protea pulchella*. Unpublished M.Sc. Thesis, University of Stellenbosch, Stellenbosch.

Lotan, JE 1967. Cone serotiny of lodgepole pine near West Yellowstone, Montana. *Forest Science* 13: 55-59.

Lyons EE, Waser NM, Price MV, Antonovics J & Motten AF 1989. Sources of variation in plant reproductive success and implications for the concept of sexual selection. *American Naturalist* 134: 409-433.

Macarthur RH & Wilson EO 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey.

Mack RN & Harper JL 1977. Interference in dune annuals: spatial pattern and neighbourhood effects. *Ecology* 65: 345-363.

Mack RN & Pyke DA 1983. The demography of *Bromus tectorum*: variation in time and space. *Journal of Ecology* 71: 69-93.

Manders PT 1990. Fire and other variables as determinants of forest/fynbos boundaries in the Cape Province. *Journal of Vegetation Science* 1: 483-490.

Manders PT & Richardson DM 1992. Colonisation of Cape fynbos communities by forest species. *Forest Ecology & Management* 48: 277-293.

Mattson WJ 1978. The role of insects in the dynamics of cone production of red pine. *Oecologia (Berlin)* 33: 327-349.

Maze KE & Bond WJ 1996. Are *Protea* populations seed limited? Implications for wildflower harvesting in Cape fynbos. *Australian Journal of Ecology* 21: 96-105.

Meney KA, Nielssen GM & Dixon KW 1994. Seed bank patterns in Restionaceae and Epacridaceae after widlfire in kwongan in southwestern Australia. *Journal of Vegetation Science* 5: 5-12.

McDonald DJ 1988. A synopsis of the plant communities of Swartboschkloof, Jonkershoek, Cape Province. *Bothalia* 18: 233-260.

Midgley JJ 1988. Mortality of Proteaceae seedlings in their first summer. *South African Forestry Journal* 145: 9-12.

Midgley JJ 1989. Season of burn of serotinous fynbos Proteaceae: a critical review and further data. *South African Journal of Botany* 55: 165-70.

Midgley, JJ & Viviers, M 1990. The germination of seeds from heated serotinous cones of eight shrubland species. *South African Forestry Journal* 155: 5-9.

Midgley JJ, Hoekstra TT & Bartholomew R 1989. The effects of date of planting on field establishment of serotinous Cape Proteaceae. *Vegetatio* 79: 185-92.

Mitchell JJ, Van Staden J & Brown NAC 1986. Germination of *Protea compacta* achenes: the relationship between incubation temperature and endogenous cytokinin levels. *Acta Horticulturae* 185: 31-37.

Montygierd-loyba TM & Keeley JE 1987. Demographic structure of Ceanothus megacarpus chaparral in the long absence of fire. *Ecology* 68: 211-213.

Mooney HA & Conrad CE (tech. coord.)1977. Proceedings of the symposium on the environmental consequences of fire and fuel management in mediterranean ecosystems. General Technical Report WO-3, USDA Forest Service, Washington DC.

Morris EC & Myerscough PJ 1988. Survivorship, growth and self-thinning in Banksia ericifolia. *Australian Journal of Ecology* 13: 181-189.

Mott JJ & Groves RH 1981. Germination strategies. In: Pate J S & McComb A J (eds.), *The biology of Australian plants*, pp 307 -341. University of Western Australia Press, University of Western Australia, Western Australia.

Musil CF 1991. Seed bank dynamics in sand plain lowland fynbos. *South African Journal of Botany* 57: 131-142.

Mustart PJ & Cowling RM 1991. Seed germination of four serotinous Agulhas Plain Proteaceae. *South African Journal of Botany* 57: 310-313.

Mustart PJ & Cowling RM 1992a. Impact of flower and cone harvesting on seed banks and seed set of serotinous Proteaceae. *South African Journal of Botany* 58: 337-342.

Mustart PJ & Cowling RM 1992b. Seed size: phylogeny and adaptation in two closely related Proteaceae species pairs. *Oecologia* 91: 292-295.

Mustart PJ & Cowling RM 1993a. The role of regeneration stages in the distribution of edaphically restricted fynbos Proteaceae. *Ecology* 74: 1490-1499.

Mustart PJ & Cowling RM 1993b. Effects of soil and seed characteristics on seed germination and their possible roles in determining field emergence patterns of four Agulhas Plain Proteaceae. *Canadian Journal of Botany* 71: 1363-1368.

Mustart PJ, Cowling RM & Dunne TT 1994. Reproductive traits of two closely related species-pairs on adjacent, different soil types in South African Fynbos. *Vegetatio* 111: 161-171.

Mustart PJ, Cowling RM & Wright 1995. Clustering of fertile seeds in infructescences of serotinous *Protea* species: an anti-predation mechanism. *African Journal of Ecology* 33: 224-229.

Mutch RW 1970. Wildland fires and ecoosystems - a hypothesis. *Ecology* 66: 51: 1046-1051.

Myburgh AC & Rust DJ 1975. Borers of economic importance in proteas (Proteaceae). Proceedings of the First Congress of the Entomological Society of southern Africa: 3-9.

Myburgh AC, Rust DJ & Starke LC 1973. Pests of protea cut-flowers. *Journal of the Entomological Society of southern Africa* 36: 251-255.

Myburgh AC, Starke LC & Rust DJ 1974. Destructive insects in the seed heads of *Protea barbigera* Meisner (Proteaceae). *Journal of the Entomological Society of southern Africa* 37: 23-29.

Nicholls N 1991. The El Niño / southern oscillation and Australian vegetation. *Vegetatio* 91: 23-36.

Pacala SW 1988. Competitive equivalence: the coevolutionary consequences of a sedentary habit. *American Naturalist* 132: 571-563.

Parker VT 1984. Correlation of physiological divergence with reproductive mode in chaparral shrubs.

Madrono 31: 231-242.

Pate JS, Meney KA & Dixon KW 1991. Contrasting growth and morphological characteristics of fire-sensitive (obligate seeder) and fire-resistant (resprouter) species of Restionaceae (s. hemisphere restiads) from south-western Australia. *Australian Journal of Botany* 39: 505-525.

Pate JS, Rasins E, Rullo J & Kuo J 1986. Seed nutrient reserves of the Proteaceae with special reference to protein bodies and their inclusions. *Annals of Botany* 57: 747-770.

Pate JS, Froend RH, Bowen BJ, Hansen A & Kuo J 1990. Seedling growth and storage characteristics of seed and resprouter species of mediterranean-type ecosystems of S.W. Australia. *Annals of Botany* 65: 585-601.

Paton DC 1983. The influence of honeyeaters on flowering strategies of Australian plants. In: *Pollination and Evolution* (eds Armstrong JA, Powell JM & Richards AJ) pp 95-108. Royal Botanic Gardens, Sydney.

Pearl R 1927. The growth of populations. *Quarterly Review of Botany* 2: 532-548.

Pickett STA & White PS 1985. *The ecology of natural disturbance and patch dynamics.* Academic Press, Orlando, Florida.

Plathe DJR & Van Der Zel DW 1969. 'n Veldbrandeksperiment op meervoudige opvanggebiede in Jakkalsrivier, Lebanon. *Forestry in South Africa* 10:63-71.

Pyke DA & Thompson JN 1986. Statistical analysis of survival and removal experiments. *Ecology* 67: 240-245.

Rebelo AG & Rourke JP 1986. Seed germination and seed set in southern African Proteaceae: ecological determinants and horticultural problems. *Acta Horticulturae* 185: 75-88.

Reznick D 1988. Costs of reproduction: an evaluation of the empirical evidence. *Oikos* 44: 257-267.

Richards MB & Lamont BB 1996. Post-fire mortality and water relations of three congeneric shrub species inder extreme water stress - a trade-off with fecundity? *Oecologia* 107: 53-60.

Richardson DM & Bond WJ 1990. Determinants of plant distribution: evidence from pine invasions. *American Naturalist* 136.

Richardson DM & Kruger FJ 1990. Water relations and photosynthetic characteristics of selected trees and shrubs of riparian and hillslope habitats in the south-western Cape Province, South Africa. *South African Journal of Botany* 56: 214-225.

Richardson DM, van Wilgen BW, Le Maitre DC, Higgins, KB & Forsyth, GG 1994. A computer-based system for fire management in the mountains of the Cape Province, South Africa. *International Journal of Wildland Fire* 4: 17-32.

Root RB 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleraceae*). *Ecological Monographs* 3: 95-123.

Rourke JP 1980. *The Proteas of Southern Africa.* Purnell, Cape Town.

Salisbury EJ 1942. The reproductive capacity of plants. Bell, London.

SAS 1985. SAS® User's guide: Basics. Version 5 edition, Cary NC: SAS Institute Inc., North Carolina, U.S.A.

SAS 1996. SAS/STAT® Software changes and enhancements through release 6.11, Cary NC: SAS Institute Inc., North Carolina, U.S.A.

Schaffer WM 1974. Selection for optimal life-histories: the effects of age structure. *Ecology* 55: 291-303.

Schaffer WM & Gadgil MD 1975. Selection for optimal life-histories in plants. In: ML Cody & Diamond JM (eds.) *Ecology and evolution of communities*, pp 142-156. Belknap Press, Cambridge Mass, and London, England.

Schaffer WM & Leigh EG 1976. The prospective role of mathematical theory in plant ecology. *Systematic Botany* 1: 209-232.

Schmid JM, Mitchell JC, Carlin KD & Wagner MR 1984. Insect damage, cone dimensions, and seed production in crown levels of ponderosa pine. *Great Basin Naturalist* 44: 575-578.

Schulze RE & Kunz PJ 1996. Climate change scenarios for southern Africa: a 1993 view. In: *Global climate change and South Africa* (ed. Shackelton LY, Lennon SJ & Tosen GR), pp 5-8. Environmental Scientific Association, Cleveland, South Africa.

Scott JK 1982. The impact of destructive insects on reproduction in six species of *Banksia* L.F. (Proteaceae). *Australian Journal of Zoology* 30: 901-921.

Shaanker RU, Ganeshaiah KN & Bawa KJ 1988. Parent-offspring conflict, sibling rivalry, and brood size patterns in plants. *Annual Review of Ecology and Systematics* 19: 177-205.

Silvertown J 1980. The evolutionary ecology of mast seeding in trees. *Biological Journal of the Linnaean Society* 14: 235-250.

Smith RE & Richardson DM 1990. Comparative water relations of selected reseeding and resprouting fynbos plants in the Jonkershoek Valley, Cape Province, South Africa. *South African Journal of Botany* 56: 683-694.

Smith RE, Van Wilgen BW, Forsyth GG & Richardson DM 1992. Coexistence of seeders and sprouters in a fire-prone environment: the role of ecophysiology and soil moisture. In: *Fire in South African mountain fynbos: species, community and ecosystem responses to fire* (eds BW Van Wilgen, DM Richardson, FJ Kruger & HJ Van Hendsbergen), pp 108-122. Springer-Verlag, Berlin.

Sonia L & Heslehurst MR 1978. Germination characteristics of some *Banksia* species. *Australian Journal of Ecology* 3: 179-186.

Southwood TRE 1977. Habitat, the templet for ecological strategies. *Journal of Aninmal Ecology* 46: 337-365.

Southwood TRE 1988. Tactics, strategies and templets. *Oikos* 52: 3-18.

Specht RL 1963. Dark Island Heath (Ninety-Mile Plain, South Australia). VII. The effect of fertilisers on composition and growth 1950-1960. *Australian Journal of Botany* 11: 67-94.

Specht RL (ed.) 1979. *Heathlands of the World. A. Descriptive studies*. Elsevier, Amsterdam.

Specht RL 1981. Responses to fires in heathlands and related shrublands. In: *Fire and the Australian Biota* (eds Gill A M, Groves R H & Noble I R), pp. 395-415. Australian Academy of Science, Canberra.

Specht RL, Rayson P & Jackman ME 1958. Dark-Island heath (Ninety-mile plain, South Australia). VI. Pyric succession: changes in composition, coverage, dry weight, and mineral nutrient status. *Australian Journal of Botany* 6: 59-89.

Stearns SC 1976. Life-history tactics: a review of the ideas. *Quarterly Review of Biology* 51: 3-47.

Stearns SC 1977. The evolution of life history traits: A critique of the theory and a review. *Annual Review of Ecology & Systematics* 8: 145-171.

Stearns SC 1989. Trade-offs in life-history evolution. *Functional Ecology* 3: 259-268.

Stock WD & Allsop N 1992. Fynbos ecosystems: a functional perspective. In: *Fire, nutrients and diversity - fynbos ecology* (ed. RM Cowling), pp 241-259. Oxford University Press, Cape Town.

Stock WD, Pate JS, Kuo J & Hansen AP 1989. Resource control of seed set in *Banksia laricina* C.Gardner (Proteaceae). *Functional Ecology* 3: 453-460.

Stock WD, Pate JS & Delphs J 1990. Influence of seed size and quality on seedling: development under low nutrient conditions in five Australian and South African members of the Proteaceae. *Journal of Ecology* 78: 1005-1020.

Stock WD, Van der Heyden F & Lewis OAM 1992. Resource availability and the structure and function of fynbos plants. In: *Fire, nutrients and diversity - fynbos ecology* (ed. Cowling R M) pp 226-240. Oxford University Press, Cape Town.

Stohlgren TJ & Rundel PW 1986. A population model for a long-lived, resprouting chaparral shrub: *Adenostoma fasciculatum*. *Ecological Modelling* 34: 245-257.

Strauss SH & Ledig FT 1985. Seedling architecture and life history evolution in pines. *American Naturalist* 125: 702-715.

Sutherland S 1986. Patterns of fruit-set: what controls fruit-flower ratios in plants. *Evolution* 40: 117-128.

Swetnam TW & Betancourt JL 1990. Fire-southern oscillation relations in the southwestern United States. *Science* 249: 1017-1020.

Taylor HC 1978. Capensis. In: *Biogeography and Ecology of Southern Africa* (eds MJA Werger & AC Van Bruggen) pp 171-229. Dr W. Junk, The Hague.

Taylor HM, Gourley RS, Lawrence CE & Kaplan RS 1974. Natural selection of life history attributes: an analytical approach. *Theoretical Population Biology* 5: 104-122.

Van Staden J 1978. Seed viability in *Protea neriifolia*. I. The effects of time of harvesting on seed viability. *Agroplantae* 10: 65-67.

Van Staden J & Brown NAC 1977. Studies on the seed germination of South African Proteaceae -a review. *Seed Science and Technology* 5: 633-643.

Van Wagner CE 1978. Age-class distribution and the forest fire cycle. *Canadian Journal of Forest*

Research 8: 220-227.

Van Valen L 1973. A new evolutionary law. *Evolutionary Theory* 1: 1-30.

Van Wilgen BW 1981. Some effects of fire frequency on fynbos plant community composition and structure at Jonkershoek, Stellenbosch. *South African Forestry Journal* 118: 42-55.

Van Wilgen BW 1984. Adaptation of the United States fire danger rating system to fynbos conditions. I. A fuel model for fire danger rating in the fynbos biome. *South African Forestry Journal* 129: 61-65.

Van Wilgen BW & Burgan RE 1984. Adaptation of the United States fire danger rating system to fynbos conditions. Part II. Historic fire danger in the fynbos biome. *South African Forestry Journal* 129: 66-78.

Van Wilgen BW & Forsyth GG 1992. Regeneration strategies in fynbos plants and their influence on the stability of community boundaries after fire. In: *Fire in South African mountain fynbos: ecosystem, community and species response at Swartboskloof* (eds Van Wilgen BW, Richardson DM, Kruger FJ & Van Hendsbergen HJ) pp 54-71. Springer-Verlag, Berlin.

Van Wilgen BW & Le Maitre DC 1981. Preliminary estimates of nutrient levels in fynbos vegetation and the role of fire in nutrient cycling. *South African Forestry Journal* 119: 24-28.

Van Wilgen BW & McDonald DJ 1992. The Swartboskloof experimental site. In: *Fire in South African mountain fynbos: ecosystem, community and species response at Swartboskloof* (eds Van Wilgen BW, Richardson DM, Kruger FJ & Van Hendsbergen HJ) pp 1-20. Springer-Verlag, Berlin.

Van Wilgen BW & Viviers M 1985. The effect of season of fire on serotinous Proteaceae in the western Cape and the implications for fynbos management. *South African Forestry Journal* 133: 49-53.

Van Wilgen BW, Le Maitre DC & Kruger FJ 1985. Fire behaviour in South African fynbos (macchia) vegetation and predictions from Rothermel's fire model. *Journal of Applied Ecology* 22: 955-966.

Versfeld DB, Richardson DM, van Wilgen BW, Chapman RA & Forsyth GG 1992. The climate of Swartboskloof. In: *Fire in South African mountain fynbos: ecosystem, community and species response at Swartboskloof* (eds Van Wilgen B W, Richardson D M, Kruger F J & Van Hendsbergen H J) pp 21-36. Springer-Verlag, Berlin.

Vlahos S & Bell DT 1986. Soil seed-bank components of the northern jarrah forest of Western Australia. *Australian Journal of Ecology* 11: 171-179.

Vogts M 1982. South Africa's Proteaceae know them and grow them. Struik, Cape Town.

Walker BH & Graetz RD (eds) 1988. Effects of atmospheric and climate change on terrestrial ecosystems. IGBO Global Change Report No. 5, IGBP Programme, ICSU.

Walker, J 1981. Fuel dynamics in Australian vegetation. In: *Fire and the Australian biota* (eds. AM Gill, RH Groves, IR Noble), pp 101-127. Australian Academy of Science, Canberra.

Waller DM 1979. Models of mast seeding in trees. *Journal of Theoretical Biology* 50: 223-232.

Weiner J & Solbrig OT 1984. The meaning and measurement of size hierarchies in plant populations. *Oecologia* 61: 334-336.

Wellington AB & Noble IR 1985. Post-fire recruitment and mortality in a population of the mallee

Eucalyptus incrassata in semi-arid, south-eastern Australia. *Journal of Ecology* 73: 645-656.

Wellington AB, Polach HA & Noble IR 1979. Radiocarbon dating of lignotubers from mallee forms of eucalypts. *Search* 10: 282-283.

Wells PV 1969. The relation between mode of reproduction and extent of speciation in woody genera of the California chaparral. *Evolution* 23: 264-267.

Westoby M 1980. Elements of a theory of vegetation dynamics in arid rangelands. *Israel Journal of Botany* 28: 169-194.

Whelan RJ & Goldingay RL 1989. Factors affecting fruit-set in *Telopea speciosissima* (Proteaceae): the importance of pollen limitation. *Journal of Ecology* 77: 1123-1134.

Williams GC 1957. Pleiotropy, natural selection and the evolutionary theories of senescence. *Evolution* 11: 398-411.

Williams IJM 1972. A revision of the genus *Leucadendron* (Proteaceae). *Contributions of the Bolus Herbarium* No. 3.

Willson MF 1983. *Plant reproductive ecology*. John Wiley and Sons, New York.

Wilson JB & Levin DA 1986. Some consequences of skewed fecundity distributions in plants. *Theoretical and Applied Genetics* 73: 113-121.

Witkowski ETF 1990. Nutrient limitation of inflorescence and seed production in *Leucospermum parile* (Proteaceae) in Cape fynbos. *Journal of Applied Ecology* 27: 148-158.

Witkowski ETF & Lamont BB 1996. Disproportionate allocation of mineral nutrients and carbon between vegetative and reproductive structures in *Banksia hookeriana*. *Oecologia* 105: 38-42.

Witkowski ETF, Lamont BB & Connell SJ 1991. Seed bank dynamics of three co-occurring banksias in south coastal Western Australia: the role of plant age, cockatoos, senescence and interfire establishment. *Australian Journal of Botany* 39: 385-397.

Wright MG 1994. Unpredictable seed set: a defence mechanism against seed-eating insects in *Protea* species (Proteaceae). *Oecologia* 99: 397-400.

Yarie J 1981. Forest fire cycles and life-tables: a case study from interior Alaska. *Canadian Journal of Forest Research* 11: 554-562.

Young TP 1981. A general model of comparative fecundity for semelparous and iteroparous life histories. *American Naturalist* 118: 27-36.

Zammit C & Hood CW 1986. Impacts of flower and seed predators on seed set in two Banksia shrubs. *Australian Journal of Ecology* 11: 187-193.

Zammit C & Westoby C 1987a. Seedling recruitment strategies in obligate-seeding and resprouting *Banksia* shrubs. *Ecology* 68: 1984-1992.

Zammit C & Westoby M 1987b. Population structure and reproductive status of two *Banksia* shrubs at various times after fire. *Vegetatio* 70: 11-20.

Zammit CA & Zedler PH 1992. Size structure and seed production in even-aged populations of *Ceanothus greggii* in mixed chaparral. *Journal of Ecology* 81: 499-511.

Zucchini, W and Adamson, PT 1984. The occurrence and severity of droughts in South Africa. WRC Report No. 91/1/84, Water Research Commission, Pretoria.